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Living life on the edge: The role of introduction and range expansion in shaping behavior of a non-native spider

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I am submitting herewith a dissertation written by Angela Chuang entitled "Living life on the edge: The role of introduction and range expansion in shaping behavior of a non-native spider." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

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Living life on the edge: The role of invasion processes in shaping personalities in a non-native spider species

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DEDICATION

To my parents
Linda and Shu Ming Chuang

And friends and family, including
Orlando Schwery, Grace Huang, and Tiffany Chiao

whose support have been invaluable

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ABSTRACT

Animal personalities describe the behavioral phenotypes of individuals that often remain relatively stable over time and contexts. Since they can account for differential dispersal tendencies, understanding how personality types are distributed across the range can lead to important characterization of expanding invasive populations. *Cyrtophora citricola* is a colonial tentweb orbweaver spider with an Old World native range that is invasive in Florida. In my dissertation, I asked whether the behavioral traits of *C. citricola* are correlated with dispersal tendencies, and whether personality types are spatially assorted across its range. I found that this spider species does indeed exhibit personality through repeatability in various behavioral traits, and that activity and exploration behaviors were correlated with the latency to engage in ballooning long distance dispersal. I also showed that individuals at the core of the established population behaviorally differ from those at the two expanding range fronts, although these two populations seem to have diverged in traits. Individuals at the leading edge of their invasive front are faster to attack a prey stimulus and more active. Those in the western population are shyer and less exploratory. These differences suggest that any landscape level range expansion processes such as spatial sorting do not always result in similar patterns of phenotypic divergence from the core population. I also compared behavioral types of native populations of *C. citricola* in their native range with those in their invasive Florida range, to better determine whether invasive populations are subject to different pressures and processes than those in the native range. Overall, personality composition at the core of the non-native range resembled that of the native population. This dissertation suggests that personality shifts across the non-native range may be more of a product of range expansion processes, rather than selective pressures from the introduction and establishment process.

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INTRODUCTION

Given the ecological and economic costs of bioinvasions (Mack et al. 2000, Pimentel et al. 2005) and increasing incidences of species introductions (Levine and D'Antonio 2003), there is a critical need to examine the dynamics of invasive range expansions. Individuals that successfully invade a new location may possess certain characteristics that predispose them to survive and even thrive in new environments (Chapple et al. 2012). One potentially important parameter is the behavior of individuals serving as propagules in introductions or those spreading from an established point. Behavior is important to consider, because it encompasses an individual's responses and interactions with its environment. It also affects individual fitness. Identifying the presence of different behavioral types within a population may be important to predicting which individuals are likely to be successful colonizers (Chapple et al. 2012).

Research on colonizing phenotypes pertaining to morphological, physiological, and life history traits has a rich history (Cwynar and Macdonald 1987, Phillips et al. 2006, Amundsen et al. 2012, Kolbe et al. 2014). While the potential role of behavior in successful invasions has been recognized (Suarez et al. 1999), much more remains to be known on how intraspecific behavioral variation contributes to successful invasions (Chapple et al. 2012). In particular, the mechanisms by which phenotypic variation in behavior affects the success of introductions and subsequent range expansions are not well established.

Recent strides in animal behavior research have increasingly focused on the role that individual behavioral variation plays in population dynamics (Sih et al. 2004). Personalities refer to consistent individual differences in behavioral traits, often applying in contexts like general level of activity, boldness in the face of predation pressure, and aggression towards prey and potential competitors (Dall et al. 2004). Thus, while individuals may exhibit stable responses to stimuli that are consistent with their particular personality type, the population as a whole may exhibit behavioral variation reflecting its composition of different personality types. The presence of "personalities" has been documented across a wide variety of taxa like birds (Duckworth and Badyaev 2007), lizards (Cote and Clobert 2007), fish (Fraser et al. 2001), including invertebrates like spiders (Riechert and Hedrick 1993, Johnson and Sih 2007, Pruitt et al. 2008, Riechert and Jones 2008, Grinsted et al. 2013).

Spiders serve as ideal study organisms, given their numerical abundance, small size, and ease of care in laboratory settings. Orbweaver spiders, in particular, can be easily detected on their highly visible webs, and their capture is aided by their poor eyesight and dropping response to disturbance. Their relatively small size and dietary requirements allows for the maintenance of hundreds of individuals in a laboratory. Given the inherent variability in behavioral responses, larger sample sizes are often needed to assess population-level patterns, which is possible with abundant invertebrate populations such as

spiders. Lastly, established protocols for assessing behavioral traits in a range of spider species suggests that substantial intraspecific behavioral variation and personalities exist (Riechert and Hedrick 1993, Pruitt et al. 2008), making them good candidates to answer questions about the differential distributions of personality types at both landscape and local spatial scales.

The role of behavior in dynamic populations can be scaled from an individual to range level by considering the composition and distribution of individual personalities. Firstly, the presence of personalities in spiders suggests that individuals have varying interactions and effects on their environment. Highly aggressive spiders, for example, often kill more prey than they will eat (Maupin and Riechert 2001), impacting local prey populations differently than less aggressive conspecifics. Boldness can determine whether heterospecific relationships with web inquilines (i.e. species that live commensally in the nest of another species) are mutualisms or amensalisms (Pruitt et al. 2012). The concern that non-native species will negatively impact native communities in their introduced range provides ecological motivations for addressing how personality traits vary across space due to selective filters present during transportation, introduction, and establishment phases, as well as processes underlying range expansion.

My dissertation research entails the investigation of behavior in invasions through a personality-based approach. I studied the movement and composition of personality types in an orbweaver spider species to understand how invasion shapes personality traits. I used four main sets of research questions to guide this work, organized as such:

Chapter 1): What are the ecological and evolutionary environments of range expansion fronts? What traits are favored in leading edge populations? What trade-offs can occur with strong dispersal-related spatial selection? What are the lasting effects of range expansion and edge phenotypes over ecological time scales?

Chapter 2): In the non-native populations of the invasive orbweaver *Cyrtophora citricola*, which behavioral responses, if any, represent repeatable personality traits? Are personality traits relating to foraging aggression, activity/exploration, and boldness intercorrelated with each other? Do mean personality scores differ between the core and leading edges? How consistent are range-level processes?

Chapter 3): Are the personality traits found at the leading edges of *C. citricola*'s range expansions correlated to dispersal behaviors? Do behaviors represent genetic or plastic responses?

Chapter 4): Do mean personality traits differ between two native populations and the non-native core population of *C. citricola*? Does latitude explain any behavioral clines in the native range?

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CHAPTER I
EXPANDING POPULATION EDGES: THEORIES, TRAITS, AND TRADE-OFFS

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Abstract

Recent patterns of global change have highlighted the importance of understanding the dynamics and mechanisms of species range shifts and expansions. Unique demographic features, spatial processes, and selective pressures can result in the accumulation and evolution of distinctive phenotypic traits at the leading edges of expansions. We review the characteristics of expanding range margins and highlight possible mechanisms for the appearance of phenotypic differences between individuals at the leading edge and core of the range. The development of life history traits that increase dispersal or reproductive ability are predicted by theory and supported with extensive empirical evidence. Many examples of rapid phenotypic change are associated with trade-offs that may influence the persistence of the trait once expansion ends. Accounting for the effects of edge phenotypes and related trade-offs could be critical for predicting the spread of invasive species and species responses to climate change.

Introduction

Shifting population ranges are a common response to climate change and a central component of biological invasions. Individuals that inhabit the leading edge of an ongoing expansion tend to encounter novel environmental conditions and may be exposed to a different set of selection pressures compared to conspecifics at the core of the range. Recent range ecology studies have drawn attention to phenotypic differences that can arise between edge and core demes (subpopulations), which have wider implications for invasion biology, conservation, and climate change research. With this synthesis, we aim 1) to summarize the ecological and evolutionary environment of range expansion fronts; 2) to review the types of traits that have been observed in organisms dispersing towards population expansion fronts and the possible life history and evolutionary trade-offs by which they are constrained; and 3) to consider the lasting effects of range expansion and edge phenotypes on populations over ecological time-scales in the context of global change.

Ecological and evolutionary environment of range expansion fronts

Dispersal and Range Expansion

Range expansions are driven by the dispersal of individuals away from a population's core, a region that has been settled long enough for population dynamics to reach a stable equilibrium. Individuals who disperse into new territory are part of an expansion wave, the leading portion of which is the front. The edge (or margin) consists of the wave front and the demes immediately behind it; between the edge and the core is an intermediate region. Dispersal is a complex process that can be considered as an individual's non-returning movement away from its birthplace, home range, breeding site, or social group that has consequences for gene flow (Ronce, 2007; Clobert et al., 2009; Travis et al., 2012). Dispersal can be limited to a specific life stage (such as plant seeds, or planktonic larvae of many aquatic invertebrates) or may be possible throughout an individual's lifespan. While we primarily focus on the wave front, dispersal occurs throughout the range of a population, with a net flow of individuals from the core and the intermediate region shifting towards the edge, even after the front has passed. The resulting gene flow can influence the intermediate and edge demes and may counteract the evolution of edge phenotypes (Kirkpatrick & Barton, 1997).

Dispersal is a three-phase process consisting of departure, transience, and settlement, where each phase can be shaped by many behavioral, morphological, and physiological factors (Ronce, 2007). Dispersal is often obligatory for non-mobile species such as plants or sessile marine invertebrates, whereas active dispersal may be a response to external conditions, individual phenotypes, or genetic predispositions (Danchin et al., 2001; Ims & Hjermann, 2001). External factors associated with dispersal include intraspecific competition, kin competition, and low habitat quality; individual variation in hormone levels, body condition, behavior, size, and life history strategies can also have an influence (reviewed in Clobert et al. (2009)). After emigrating, the individual travels across the landscape. Most animals can evaluate potential habitat viability when dispersing; while the entire unsettled landscape may be suitable in some invasions, heterogeneity in habitat quality is much more likely (Wiens, 2001). This can be particularly important for range expansions following a shifting climate envelope, where edge patches may become thermally suitable at different times. Biotic factors such as conspecific density or predator presence may also influence site choice (Clobert et al., 2009). Once the organism settles, it becomes part of the new deme and may begin to adjust to local conditions. While plants are generally unable to avoid unsuitable settlement sites in the transit stage, many species are able to persist in the seed bank for long periods of time until conditions improve.

Individuals overcome the costs and risks associated with each phase of dispersal to expand into new territories successfully. These can include the resources expended gathering information (when deciding on departure or searching for a new settlement), the time and energy spent on movement, the increased risk of death or injury while in transit, the time required to acclimate, and the possible loss of local adaptation (reviewed in Bonte et al. (2012)). Dispersal may also involve indirect costs, such as resources used to improve dispersal ability or mitigate direct costs (Travis et al., 2012). These can include enhanced movement (Hill et al., 1999) or improved sensory mechanisms (Merckx & Van Dyck, 2007) in animals and altered seed mass or release heights (Levin et al., 2003) in wind-dispersed plants. Finally, dispersers are subject to opportunity costs, the benefits and activities (such as reproduction) the organism is unable to engage in because it is dispersing.

Despite the risks, dispersal can still be beneficial. Within non-expanding populations, dispersal can allow individuals to reduce the fitness cost of kin competition by lowering the density of relatives in a single location (Lambin et al., 2001). This also decreases the chance of inbreeding and the probability of lineage extinction due to localized catastrophic events (Gandon, 1999). In an expanding population, dispersal towards the edge allows individuals to escape from conspecific and kin competition by taking advantage of the benefits provided by lower population density (Bowler & Benton, 2005). Long distance dispersal towards scarcely populated demes also reduces pressures from natural enemies, including predators, parasites, and pathogens.

Demographic features of range margins

Expanding populations form a density gradient that ranges from near carrying capacity in the core to near zero at the front (Figure 1; Phillips et al., 2010; All tables and figures are located in the appendix). This density change can lead to selection for different life history trade-offs. High-density demes experience greater intraspecific competition, which generally selects for life histories that favor competitive ability or efficient resource use at the expense of reproductive rate (Phillips et al., 2010). Conversely, low-density demes with fewer resource constraints can maximize fitness by greater reproductive investments (Reznick et al., 2002). These trade-offs can have varied mechanisms; for example, core individuals may produce fewer offspring with larger body sizes and higher survival rates, or they may use low-quality resources that in other circumstances would not be worth the effort to acquire (Honěk, 1993; Svanbäck & Bolnick, 2007).

Expanding populations tend to be structured by dispersal ability among actively dispersing species (Figure 2; Shine et al., 2011). As the population disperses, variation in dispersal ability limits the maximum distance that individuals can travel; thus, the best dispersers determine the location of the front. Since membership of edge demes depends on high dispersal ability, the

top dispersers will reproduce with each other (the Olympic Village effect) (Phillips et al., 2008). If the dispersal-enhancing phenotype is heritable, edge offspring should be better dispersers than offspring nearer the core. As the offspring still have variation in dispersal ability, the process repeats. This runaway assortment of dispersal ability creates a positive feedback loop leading to the evolution of a continually increasing expansion rate (Phillips et al., 2010).

Range edges may also exhibit demographic Allee effects, where individual fitness decreases due to low population density (Stephens et al., 1999). A major cause of this is the reduction in conspecific cooperation, facilitation, or access (Courchamp et al., 1999), which could result in difficulty finding mates (Wells et al., 1998), increased cost of cooperative parental care (Clutton-Brock et al., 1998), or a lower effectiveness of collective anti-predator behaviors (Quinn et al., 1993). Increased demographic stochasticity (including imbalanced sex ratios) may produce similar patterns (Stephens et al., 1999). Positive density-dependence can slow edge dispersal (Lewis & Kareiva, 1993; Kot et al., 1996), with strong Allee effects (where demes below a critical density are completely unable to propagate) halting range expansion until further immigrants from the core arrive (Keitt et al., 2001). This can limit an otherwise accelerating rate of invasion and counteract the increasing dispersal capability promoted by spatial sorting (Travis & Dytham, 2002). Therefore, demes slightly behind the front may experience the greatest rate of growth, as they are unaffected by the drawbacks of either negative or positive density dependence (South & Kenward, 2001). Because Allee effects generally do not apply to organisms that do not rely on conspecifics for establishment or reproduction, reproductively-assured, self-compatible individuals are more likely to establish colonies than self-incompatible ones (Baker, 1955; Cox, 1989). Therefore, we predict that parthenogenetic animals and self-fertilizing or clonally reproducing plants will be relatively unaffected by low population density and can expand more rapidly at the wave front.

Genetic Processes at Expanding Margins

Low densities and spatial sorting can also influence an expanding population's genetics. As the leading edge expands, it undergoes repeated founder effects that produce a spatial pattern analogous to genetic drift (Slatkin & Excoffier, 2012). A small portion of the alleles that arise near the margin will survive and disperse, "surfing" (Figure 3) along the moving wave front and attaining much higher frequencies than would be expected in a stable population (Edmonds et al., 2004; Klopfstein et al., 2006). Although this process is most easily observed with new mutations, it can affect any allele in the population, allowing dramatic shifts in standing variation (Excoffier et al., 2009). There are few empirical studies examining allele surfing, and its prevalence in sexually reproducing animals is currently uncertain (Goodsman et al., 2014); however, associated patterns have been inferred from historical expansions of strawberry

poison-arrow frogs (*Dendrobates pumilio*)(Gehara et al., 2013), spurred-thighed tortoises (*Testudo graeca*) (Gracia et al., 2013), and humans (Sousa et al., 2014).

Alleles can surf regardless of their effects on fitness. Beneficial alleles will spread much more quickly towards the edge than the core. Deleterious alleles that would disappear from a static population may drift to fixation at the edge; these can then propagate along the expanding front despite negative fitness effects (Travis et al., 2007). Although these mutations will eventually be replaced by advantageous alleles from the core, recently established demes often exhibit an "expansion load" of deleterious alleles that can persist for thousands of generations (Peischl et al., 2013).

Allele surfing is a potential genetic mechanism underlying the evolution of life history traits at expanding range margins. Individual-based simulations predict new mutations at the edge are more likely to surf along the wave front if they increase dispersal capability (Travis et al., 2010). Although a high rate of dispersal mortality can create a trade-off between dispersal distance and surfing probability, the front still evolves the maximum dispersal distance. When additional life history trade-offs are incorporated into these models, the expanding front evolves increased dispersal and fecundity at the cost of competitive ability (Burton et al., 2010).

Limitations of Current Theory

In principle, these ecological and evolutionary processes should apply to both invasions and climate change; however, most theoretical work to date on this subject involves invasion-like models of a single species expanding through an unchanging region of suitable habitat. This scenario ignores additional ecological factors that may limit evolution in climate shifts (Moran & Alexander, 2014). Populations often expand over fragmented or disturbed landscapes with varying habitat suitability; they may also encounter novel environmental conditions to which they are not well-adapted. For climate-induced range shifts, marginal demes are also limited by a shifting envelope of suitable climate, opposing over-dispersers moving beyond the habitable zone and under-dispersers falling behind the lagging edge (Boeye et al., 2013). Given that climatic suitability envelopes generally shift slowly when compared to invasion speeds, invasive populations would be expected to develop more extreme expansion-promoting traits than climate-shifting populations.

Interspecific interactions can also affect range expansion dynamics. For example, the presence of an established competitor in the invaded territory is expected to reduce the degree to which population's dispersal increases (Burton et al., 2010). Estimating the effects of biotic interactions is particularly complicated in climate change scenarios, where entire communities are expected to shift (Urban et al., 2013). Since not all species will move at the same speed or even in the same direction (Gillings et al., 2015), relationships at edge demes

could break down and may lead to novel selective pressures. Populations that disperse faster than populations with which they have specific relationships will need to either change the relationship at the edge (by switching to a substitute species or losing the relationship entirely) or be limited by the slower disperser's speed. Ecological niche models of avian communities, for example, have projected a decrease in functional diversity (Barbet-Massin & Jetz, 2015) and substantial changes in dietary guild composition (Ko et al., 2014), with more severe changes occurring with higher dispersal rates. The degree to which trait shifts at range edges could affect these complex community dynamics remains mostly uninvestigated and is a promising avenue for future theoretical investigations.

The expected patterns of leading edge differences in phenotype and genotype are often supported by empirical case studies drawn from the invasion biology and climate change literature. In the next section, we report trait differences across expanding ranges found in the invasion, colonization, and climate change literature, where leading edge individuals often differ from their conspecifics at the core. Spatial assortment of individuals across a diverse range of taxa is found by dispersal ability, which often relates to the differences in life history characteristics, morphology, behavior, and physiology observed among edge and core demes (Table 1). While we focus on case studies in which phenotypic trait differences occur, some studies find no changes between demes at the expanding range edge and core (Table 2). Owing to publication biases against studies reporting null results and increased difficulties in identifying such studies during the literature search process, more case studies likely exist than are presented here.

What types of traits accumulate at range expansion fronts?

Morphology

In general, dispersal-promoting traits are more common in range edge individuals than core individuals. Since active dispersal is a process often requiring extended physical exertion and activity, individual morphology plays a defining role in locomotive and, by association, dispersal ability. Across a wide range of taxa, active dispersal ability generally involves larger individual size or better body condition (Lawrence, 1987), and the same is often true for individuals found in leading range edges (fish (Cote et al., 2010; Lopez et al., 2012), birds (Gunnarsson et al., 2012), insects ((Hill et al., 1999)), nematodes (Kelehear et al., 2012). Larger individual size or biomass may facilitate dispersal if the physical exertion required is great enough to demand more than just a minimal amount of stored reserves. If travel precludes foraging opportunities to sustain dispersal, then individuals with greater initial repositories of fat are more likely to survive an imposed fast (Lindstedt & Boyce, 1985; Bowler & Benton, 2005).

When larger body lengths and sizes are correlated with dispersal ability, individuals at the leading edge of range expansions tend to outsize their counterparts in core demes. Invasive cane toads (*Rhinella marina*) in Australia remain the classic example of a species exhibiting morphological trait shifts along an expansion gradient; individuals at the vanguard of the invasion front possess longer legs on average, which promotes further displacement (Phillips et al., 2006). Enhanced locomotive abilities in these anurans is linked to the rate of their spread, which has increased over time (Phillips et al., 2007). Successive generations of toads at the range front have been dispersing at a faster rate; a five-fold increase in the rate of annual range expansion has been observed between the 1940s and early 2000s. Cane toads also provide strong support for the “Olympic Village effect”, in which spatial sorting processes result in a high proportion of strong dispersers at the leading edge. Resulting offspring from leading edge copulations exhibit heritable dispersal traits, such as longer average femur length, thereby forming a new generation of strong dispersers that will maintain or strengthen spatial sorting in the population (Figure 2).

Dispersal-related morphological changes in leading edge individuals have been most frequently demonstrated in insects, where individuals found at range edges can exhibit larger thorax sizes and volumes than conspecifics at the core (butterflies (Hill et al., 1999; Braschler & Hill, 2007), beetles (Laparie et al., 2013), ants (Abril et al., 2013)). Since insect flight muscles are located within the thoracic cavity, smaller thoraxes constrain flight muscle size and flight ability (Berwaerts et al., 2002). Selection on the enhancement of traits like leg length, thorax size, and abdomen size is demonstrated in the case of the flightless predatory ground beetle, *Merizodus soledadinus* (Laparie et al., 2013). While leg length and thorax size are indirect measures of locomotor abilities, abdominal size is widely considered to be a proxy for energy stores in insects. Extensive surveys of this invasive species on the Kerguelen Islands over time have revealed a positive relationship between range expansion distance and increasing body size parameters, including elytra length, head length, as well as pronotum length and width.

Dispersal-related morphology occasionally occurs in discrete forms, as is best documented in grasshoppers and crickets (order Orthoptera). Populations of such species are comprised of both the prevalent brachypterous (short-winged) forms and rarer macropterous (long-winged) forms. While brachypters are limited in dispersal ability, macropters are able to engage in strong pulses of long-distance range expansion under favorable environmental conditions (Hochkirch & Damerau, 2009). Multiple studies have reported higher proportions of macropterous individuals at recently colonized range fronts, suggesting that these dispersal-oriented morphs may act as the initial colonists prior to population establishment (crickets (Thomas et al., 2001; Simmons & Thomas, 2004; Poniatowski et al., 2012), beetles (Niemela & Spence, 1991; Niemela & Spence, 1999)). Not only can the frequency of dispersal morphs differ across an

expanding range, but the dispersal ability of macropterous individuals may be elevated at the margins. Simmons and Thomas report a case of long-winged conehead bush cricket (*Conocephalus discolor*) macropters from the leading edge with fourfold flight endurance compared to macropters at the core of the population (2004). Faster rates of range expansion over time further support the possibility that this species has undergone a recent selection for dispersal-related phenotypic changes along the leading edge.

In wind-dispersed plants, diaspore morphology is a strong determinant of passive dispersal ability (Platt & Weis, 1977; Morse & Schmitt, 1985; Augspurger & Franson, 1987; Andersen, 1993). A diaspore consists of a seed and additional plant tissue that assists in dispersal. Such additions include wings, pappi, and plumes that can allow seeds to glide, rotate, or enhance drag (Andersen, 1993), facilitating further displacement. The speed at which they fall and their corresponding distance from their source are related to the size and weight of the diaspore (Sheldon & Burrows, 1973) as well as plume and wing loading (Matlack, 1987). Plume and wing loading refer to the ratio of the seed mass to its area (Vogel & Vogel, 1994), where decreased plume and wing loading is correlated to greater dispersal potential (Andersen, 1993). Consistent with patterns of greater dispersal ability at range margins, seeds measured from the edge tend to have decreased mass, plume loading (Huang et al., 2015), and wing loading (Cwynar & MacDonald, 1987) (Table 1). Feathery structures like the pappus in diaspores are also larger (Monty & Mahy, 2010), which increases air drag and prolongs the period of descent, resulting in further displacement.

Metabolism

Patterns in metabolic activities also differ between leading edge and core demes. Faster growth rate at range edges is a response demonstrated by a variety of taxa (amphibians (Lindström et al., 2013), crustaceans (Sanford et al., 2006), fish (Bohn et al., 2004; Carol et al., 2009), insects (Bartle et al., 2013)). Rapid growth may be important for colonizers in order to attain an optimal size over a shorter time period for dispersal, predator defense, and foraging purposes (Sebens, 1982; Marshall & Keough, 2003). This is facilitated by higher feeding rates, as is seen by cane toads at their invasion front (Lindström et al., 2013). Faster growth is associated with earlier sexual maturation and shorter generation time (Metcalfe & Monaghan, 2003), which may promote population growth and the persistence of low-density settlements. Alternatively, faster growth coupled with abundant resources may lead to the attainment of greater biomass and size in leading edge individuals, which may aid both in continued dispersal efforts and defending new territories. Metabolic shifts between core and edge demes may thus be coupled with changes in life history characteristics.

Life history

Changes in life history, especially with regard to reproductive strategies, are also predicted in leading edge individuals. Reproductive life history changes reported in the literature match theoretical expectations of shifts towards greater reproductive output at some edge demes, which may aid in the establishment of a species in a novel environment. Such changes may occur independently of dispersal ability and expansion processes, as may be particularly relevant in the case of organisms that disperse passively. Besides shifting life histories towards faster sexual maturation (Sanford et al., 2006; Amundsen et al., 2012; Kelehear et al., 2012), studies have reported individuals at expanding range edges with greater reproductive output (Amundsen et al., 2012) and investment in reproductive tissue (Ling et al., 2008) compared to their core population counterparts. These reproductive changes may promote the chances of survival and establishment in demes at the front of a range expansion until carrying capacity is reached.

Life history shifts can also apply to dispersal timing, especially in species that undergo dispersal during particular life stages or prior to sexual maturation. In Eurasian beavers (*Castor fiber*), range edge individuals initiate dispersal at a younger age (Hartman, 1997a), as previously predicted in low-density, colonizing populations (Parsons & Brown, 1979). At least five of the nine beavers in this study dispersed precocially as yearlings, although this generally occurs at two years of age (Sun et al., 2000; McNew & Woolf, 2005). Three yearlings showed exploratory movements by temporarily leaving their natal territory, and at least one female had given birth by her second year (Hartman, 1997a), where parturition age ranges between two to five years (Doboszynska & Zurowski, 1983). Although this study is limited in scope and sample size, it emphasizes the possibility of life history shifts in species with life stage-dependent dispersal and highlights the importance for more detailed investigations in such phenomena. Life history shifts that speed up the age of dispersal and reproduction can also serve to increase the rate of colonization, by decreasing the generational time between advances into new territory.

Behavior

Recent interest in animal personality traits has led to a corresponding growth in the literature regarding the role of behavior in range expansions and invasions (Chapple et al., 2012; Lopez et al., 2012; Liebl & Martin, 2014). Since behavior affects an individual's response to internal and external stimuli, differing environmental conditions may select for particular behavioral phenotypes that promote persistence at range edges and novel habitats. Such traits may be independent of expansion-promoting traits like dispersal tendency. Aggression in particular has been linked as driver in successful range expansions (Hudina et al., 2011), since enhanced aggression may promote territory and resource acquisition from both heterospecifics and conspecifics in new habitats

(Duckworth & Badyaev, 2007; Hudina et al., 2011). Traits associated with lower neophobia (fear of novelty) and an increased tendency to exploit novel resources and environments will similarly confer advantages to individuals who enter a new territory and/or encounter conditions for which they have no evolutionarily-primed response for. Exploration of novel environments allows individuals to identify not only potential resources like food (Cole & Quinn, 2012), but also sources of danger such as predators and inhospitable abiotic conditions. This has been demonstrated in the more exploratory tendencies of house sparrows (*Passer domesticus*) inhabiting the edge of their introduced Kenyan ranges when compared to their core counterparts (Liebl & Martin, 2012).

Covariation of behavioral traits such as aggression with dispersal tendency can result in a population spatial structure based on differing behavioral types. Behavioral syndromes are suites of correlated behaviors which remain consistent over various contexts, such as foraging, mating, and brood care (Sih et al., 2004). Recent work on behavioral syndromes has linked dispersal tendency to various behaviors such as boldness, aggression, exploratory tendency, activity level, and sociality (Sih et al., 2004; Duckworth, 2006; Cote et al., 2010). The coupling of two or more behaviors that are advantageous in edge or novel habitats may lead to distinctive edge phenotypes that drive continued range spread. Duckworth (2006) reports a case in male bluebirds (*Sialis mexicana*) in which aggression and asociality are both linked to dispersal tendency. Asocial males are more likely to leave their natal territory, successfully establish a territory, and aggressively defend their nest against both congeners and male conspecifics. Alternatively, social males are more likely to remain in their birthplace or disperse in groups; thus, later waves of colonization are often comprised of social behavioral types. These individuals then settle in former frontier territories, where their asocial counterparts have already successfully driven out congeneric competitors. Thus, the coupling of dispersal, aggression, and asociality in this bird species has facilitated the successful recolonization of its historical native range, since dispersive individuals are also behaviorally suited for edge conditions.

Physiology

Range expansion processes may exert physiological pressure on edge individuals undergoing long bouts of dispersal or encountering unfamiliar environments. This is particularly true when a species' range exists along an environmental gradient, where new edge territory includes novel abiotic and biotic conditions to immigrants. There, individuals can encounter new objects including novel nesting spaces, food sources, predators, and parasites, as well as new visual, auditory, chemical, and tactile stimuli. Range edge immigrants are predicted to exhibit physiological differences in stress responses due to more frequent exposure to novel objects and stimuli, which act as environmental stressors. For example, house sparrows regulate corticosterone differently

across their introduced Kenyan range (Liebl & Martin, 2012). Sparrows farther from the range core release more corticosterone in response to exposure to stressful environmental conditions. This is hypothesized to increase vigilance to new environmental stimuli and aid in memory formation associated with new experiences (Dekloet, 1991). The increased release of corticosterone may thus assist range edge individuals in remembering consequences of novel experiences to better respond in future encounters.

Environmental stress in the form of climatic differences can also prompt physiological responses in expanding populations. This selects for colonizing individuals with the physiological means of enduring, if not thriving, in new locations. For instance, invasive brown anole lizards (*Anolis sagrei*) have a lower critical thermal minimum threshold at the northward edge of their introduced range in the southeastern United States (Kolbe et al., 2014). This ability to withstand cooler temperatures is necessary for leading edge individuals that continue dispersing beyond their normal thermal range. Additionally, maximal thermal tolerance in brown anoles remains unaffected, suggesting an acclimation towards a wider range of temperatures compared to core conspecifics. Range edge anoles also have a lower mean water loss rate, which may be important for drought tolerance or desiccation resistance (Kolbe et al., 2014). The case of the brown anole illustrates the ability of organisms to broaden their physiological tolerance to accommodate new environmental conditions. Given the ongoing influx of studies on climate change-driven range expansions, we expect to find additional cases of both thermal physiological shifts and extensions, although not all taxa may have the potential to make such rapid physiological shifts (Ling et al., 2008).

Absence and variation of trait shifts

Several case studies reported no trait changes at the edge (Table 2). While it is possible that the expanding population is not undergoing any phenotypic shifts, some studies may simply have failed to detect a change. Inappropriate methodology may introduce bias; for example, capture techniques may preferentially capture larger individuals, causing non-random sampling. If trait changes are small (such as would be expected at the beginning of an expansion) or individual variation is high, large sample sizes are needed to attain sufficient statistical power to assess the effect. Since distinct phenotypes or life history characteristics may only be present at certain life stages, seasons, or times of day, temporal factors must also be considered when designing a study. Investigators may also focus on the wrong trait, such as taking morphological measurements when physiological differences exist instead. Others have measured a variety of traits could hypothetically undergo spatial sorting or selection, such as body pigmentation and patch size (Cardoso et al., 2014). While some traits, such as breast pigmentation and mask area have undergone sexual selection in common waxbills, other measured traits like color saturation

in the bill or red area on the breast may not have biological relevance for the underlying processes.

Lastly, the age of the expanding range boundary and the definition of the "edge" must be considered. If edge traits are ephemeral in nature, measuring them early on or towards the end of the range expansion process may lead to an inability to detect changes. Similarly, an overly broad definition of the "edge" will lead to the inclusion of intermediate phenotypes that can similarly obscure spatial sorting patterns.

Many of these reviewed phenotypic shifts can be readily classified as adaptive traits, which facilitate adjustment to novel conditions at the edge, or expansion traits, which improve the deme's range-shifting ability (Table 1). For example, changes in dispersal ability and thermal tolerance are expansion and adaptive traits, respectively, as the former drives the range expansion process and the latter promotes persistence in the new environment. There are some areas in the empirical literature, particularly for reproduction-associated traits, where these classifications are not mutually exclusive. While higher fecundity facilitates expansion by increasing population growth, it can also be more adaptive if a competitor is present in the new range (Burton et al., 2010). Expansion traits undergoing spatial sorting are almost always expected to continue favoring dispersal (e.g. longer rather than shorter legs) until stronger selective forces come into play. Due to variation in local conditions at the edge, it is more challenging to make broad generalizations about the evolution of adaptive traits during range expansions, although predictions about specific populations are still feasible if sufficient ecological context is known.

Differing ecological context could potentially explain some of the apparently conflicting patterns among the studies in this review. In some cases, leading edge phenotypes are temporally-dependent patterns associated with the breeding period (Liebl & Martin, 2012) or season (Gutowsky & Fox, 2011). Interactions between the timing of specimen sampling or collecting and certain observed phenotypes highlight the importance of considering the phenology and different life history contexts of the study organisms in question. For example, investigations of invasive round goby (*Neogobius melanostomus*) populations have produced conflicting leading edge patterns both among and within studies (Gutowsky & Fox, 2011; Brownscombe & Fox, 2012; Groen et al., 2012). Gobies at the edge are significantly larger when sampled in the autumn, but display no discernible pattern in the summer (Gutowsky & Fox, 2011). Given the dynamic nature of leading edges, tracking populations over both short and long time scales is critical for understanding broader ecological and evolutionary patterns. Different findings among separate populations of the same species could also reflect adaptive responses to geographically-specific ecological factors such as resource abundance or predation pressure, which could lead diverging leading edge dynamics. In other words, round gobies introduced to a river system in

Ontario, Canada may differ from those in the Gulf of Gdansk in Poland due to interactions with locally distinct biotic and abiotic factors.

Are there trade-offs associated with dispersal or life history-related changes at range edges?

An investigation of traits along a range expansion is not complete without consideration of associated trade-offs, since they may suggest constraints, mechanisms, and strategies underlying energetic allocations to traits (Ricklefs & Wikelski, 2002; Ardia, 2005). Life history theory suggests that trade-offs are products of competition for limited time and resources between different processes within an individual (Zera & Harshman, 2001). As a consequence, allocations of resources towards one trait necessarily result in a lost opportunity for the enhancement of another. Rapid changes in life history and dispersal ability raise the question of whether continual selection for certain traits can continue indefinitely or if it will eventually be constrained by life history trade-offs. While few studies thus far have explicitly sought to address the costs of range expansion on individuals within a population, there is nonetheless a good record of the negative impacts of colonization pressures on individual organisms. Given the energetically-costly nature of dispersal or enhanced reproductive effort common at range edges, we expected to find limits on the enhancement of range-edge traits through selection; these constraints would manifest in the form of life history trade-offs. Indeed, many of the examples narrated in the previous section were incomplete. Leading edge demes can encounter complications associated with their phenotypic trait changes or experienced problems endemic to range margins that lead to negative changes in individual life quality and reduced fitness (Table 3).

Longevity and Health

The survival, longevity, and/or overall health of leading edge individuals can be negatively impacted by rapid changes in dispersal or life history traits. For instance, organisms with faster growth rates and earlier sexual maturation tend to have a shorter life span. Invasive vendace fish (*Coregonus albula*) from a recently colonized lake were reported to be comprised of individuals maturing at a younger age and smaller size, displaying characteristics of a "live fast, die young" life style (Amundsen et al., 2012). Besides allocating resources towards reproduction instead of body mass, colonist fish experienced an annual mortality of 71-75%, as opposed to 43-60% in the source population.

Despite being a well-studied topic, the reasons and mechanisms behind this trade-off between growth and lifespan is not clear (Metcalfe & Monaghan, 2003). Individuals undergoing faster growth require more food, and increased foraging effort carries greater risks of capture by predators due to greater

exposure in the open (Gotthard, 2000). Another hypothesis posits that faster growth generally requires a faster metabolic rate, which can be difficult to down-regulate at sub-optimal environmental conditions (Arendt, 1997). In other words, individuals with a higher metabolism may be more vulnerable to starvation-induced stress (Blanckenhorn, 2000), which occurs when resources are not abundant or if environmental conditions prevent foraging activities (e.g. poor weather). From a mechanistic perspective, rapid individual growth may cause stress on a cellular level; faster growth has been linked to oxidative stress (Rollo, 2002), reduced investment in protein maintenance (Morgan et al., 2000), and reduced investment in cellular repair (Cichon, 1997). Any and all of these processes can be linked to the early-onset senescence and mortality in this observed trade-off.

Trade-offs in resource allocation may also lead to a growth-immune system trade-off, a well-documented phenomenon in natural and experimental systems (Saino et al., 1998; Soler et al., 2003; van der Most et al., 2011). Immune function may be reduced in individuals experiencing higher growth rates owing to the substantial energetic and nutritional demands associated with the maintenance of an active immune system (Lochmiller & Deerenberg, 2000). Consistent with the predictions of this phenomenon, cane toads studied from the invasion front show reduced immune function through higher rates of spinal infections (Brown et al., 2007; Skelly, 2007). In addition, about 10% of individuals at the leading edge are afflicted with spinal arthritis, a condition severe enough to impede their locomotion, especially when the vertebrae are fused (Brown et al., 2007). Most strikingly, spinal arthritis has not been observed in established core populations and is found only in individuals arising from repeated generations of spatial sorting. It appears that the rapid evolution of dispersal-related traits in this species, including longer leg length, larger body size, and faster movement, has imposed serious health costs on some individuals for which they have no compensation, strongly impacting their quality of life.

Reproductive Success

Differences in reproductive success between leading edge and core individuals represent a serious trade-off that underlies shifting dynamics between different life history strategies in a population. Trade-offs between dispersal and reproduction are reported in different contexts, ranging from behavioral to morphological. For instance, lower fitness was reported in male bluebirds that disperse more successfully (Duckworth, 2006). Since increased dispersal tendency is correlated with heightened aggression and asociality in this species, two different behavioral strategies emerged between the solitary, aggressive males and their social, less aggressive counterparts. Asocial individuals dominate the range edges, successfully establishing new territories by driving out congeneric competitors and vigorously defending their territory, but they experience lower individual fitness than their social counterparts at the core

(Duckworth & Badyaev, 2007). These aggressive, vigilant nest defenders provide less parental care, manifesting a trade-off between time spent in each activity (Duckworth, 2006). Asocial males provision their female mates with fewer resources during the incubation period, leading to lower rates of successful incubation and fewer fledged offspring. Successive migrations of social conspecifics into former frontiers (i.e. the intermediate demes) leads to a switch in the population phenotypic distribution, in favor of bluebirds with better parental skills over those with heightened aggression and defensive skills.

A classic example of trade-offs between dispersal ability and reproductive potential in a morphological context is in macropterous and brachypterous insect morphs. The high energetic cost of enhanced wing morphology and flight musculature in macropters often precludes high reproductive output. Given a finite energy acquisition rate, resources allocated to flight muscles constitute a loss in investment towards reproduction, such as in ovarian tissue mass (Kennedy, 1961). This trade-off has been well supported by comparative studies in macropterous forms of crickets (Roff, 1984; Mole & Zera, 1993), grasshoppers (Ritchie, 1983), planthoppers (Denno et al., 1989), aphids (Dixon & Howard, 1986), seed bugs (Solbreck, 1986), waterstriders (Muraji & Nakasuji, 1988), and weevils (Utida, 1972). Macropterous individuals at the leading edge of range expansions are not exempt from this trade-off, as long-winged coneheaded bush crickets demonstrate (Simmons and Thomas, 2004). On average, brachypterous females of this species weigh more and produce more eggs compared to their macropterous counterparts. The potential fitness consequences of this trade-off may explain the pronounced changes in wing morph distribution across the colonization history of their range; long-winged morphs are eight times more abundant than short-winged crickets at new range edges, but become rare in the years after successful establishment in a new landscape. Given the high reproductive costs to these dispersal-oriented morphs, population demographics may favor individuals with higher reproductive output and lower dispersal abilities after initial establishment (Zera & Denno, 1997; Travis & Dytham, 2002).

Density-dependent factors also provide further barriers to reproductive success. Sex-biased dispersal ability in several populations leads to uneven sex ratios at the leading edge, with consequences similar to an Allee effect (crustaceans (Hudina et al., 2012), fish (Gutowsky & Fox, 2011), insects (Contarini et al., 2009; Miller & Inouye, 2013)). In each of these cases, males have greater dispersal propensities and wide-tailed dispersal kernels, leading to higher ratios of males to females at range edges. Accordingly, the individuals that disperse the furthest are the least likely to encounter suitable mates in their new habitat. This likely results in either fiercer intraspecific competition when there are a few females present or no mating opportunities at all.

This type of density-dependent limitation in reproduction may be associated with slow range expansion; males with dispersal abilities that are above-average but not extraordinary are able to benefit from reduced resource

competition at the edge but still have access to mates. Even with equal sexual representation along a range edge, low population density can impede reproductive success, by extending the duration of mate searching, simply due to fewer encounters with conspecifics (Courchamp et al., 1999). Because many species have a limited window of time for reproduction, difficulty in searching for and securing a mate may lead to reproduction past an optimal period. Reproduction in senescent individuals past their reproductive prime has been associated with lower fecundity and offspring viability, all of which have fitness consequences for low-density populations (Heimpel et al., 1998).

Sexual selection against range edge-associated traits will also exert reproductive costs, with implications for continued range expansion. Icelandic black-tailed godwits (*Limosa limosa islandica*) are shorebirds that exhibit spatial structuring by male morphology, where larger males disproportionately occupy new sites at their range margins. Not only do larger males disperse further, but these overall spatial patterns are thought to be driven primarily by female preference for smaller males and the high-quality sites that they hold. Thus, larger, unsuccessful suitors tend to relocate from natal breeding grounds and suffer lower reproductive success at edge sites with lowered female abundance and site quality (Gunnarsson et al., 2012). In instances where sexual selection favors core-associated phenotypes, continued range expansion can expected to be limited. Strong female preferences for core phenotypes result in uneven sex ratios at the leading edge, if female choice leads to limited dispersal from the core.

As these studies demonstrate, trade-offs associated with traits promoting dispersal or an accelerated life history occur and may limit the range expansion process. Density-dependent reproduction limitations likewise exert a cost on leading edge population growth. The absence of reported trade-offs in other range expansions reviewed here suggest three possibilities: that trade-offs were either not considered by the researchers or were out of the scope of their study; that leading edge traits had not diverged enough for a trade-off to become apparent; or that trade-offs may not exist for all populations that experience phenotypic trait shifts across a range expansion. A more likely amendment to the last scenario may be that whatever costs incurred by phenotypic trait changes are surmounted through other mechanisms. An unequal cost-to-benefit ratio could favor the development of edge-selected traits because any drawbacks are negligible when compared to the potential gain. Future studies will ideally further investigate the processes that constrain trait evolution at expanding range edges.

Long-Term Implications

Range expansion cannot continue indefinitely. Eventually, the front will reach an area where environmental changes are too extreme for the expansion wave to cross at its current rate. When the selective pressures change too

rapidly over a small spatial scale, the front will be unable to continue expanding until it adapts to new conditions (Kirkpatrick & Barton, 1997). Local adaptation at the edge will be swamped by continued flow of core-adapted alleles, effectively leading to outbreeding depression that prevents further expansion. Populations undergoing spatial sorting for lengthy periods will have higher dispersal rates, which will result in individuals traveling farther along environmental gradients during their lifespan. The higher the expansion rate, the greater the difference in environmental conditions will be between an individual's start and end points. Therefore, spatial sorting can hamper a population's ability to adapt to new environmental conditions and can promote the formation of long-term range boundaries (Phillips, 2012).

Recently expanded populations may form a fine-scale genetic structure that is not present at the population core (Short & Petren, 2011). If two different alleles surf along distant points of the front, they can leave distinct sectors of low genetic diversity in their wake (Hallatschek et al., 2007). Over time, gene flow between these sectors will transition their boundary into a gradient that runs perpendicular to the direction of expansion, which could potentially be misinterpreted as a response to environmental variation. The abrupt shift in allele frequencies caused by genetic surfing also produces a pattern that is difficult to distinguish from selective sweeps, which could serve as a confounding factor in studies investigating selection in a phylogeographic context (Excoffier & Ray, 2008).

As a population continues to expand, the wave front will move past the demes that were previously at the edge. Newly intermediate demes will quickly begin to increase in density, due to both local births and immigration from the core. As deme size begins to approach the carrying capacity, the relative fitness of different life history strategies may begin to shift. Gene flow will introduce a large number of alleles from the core and shift highly dispersive alleles towards the edge. We predict that the strength of these changing demographic, ecological, and evolutionary pressures will determine whether the edge phenotype is ephemeral or persistent (Figure 4). Ephemeral traits arise along the edge but shift back towards the core phenotype once the wave front passes, while persistent traits are maintained despite changing demographics. In theory, expansion traits that have negative life history trade-offs are more likely to be ephemeral (Burton et al., 2010), while persistence is more likely in adaptive traits that facilitate colonization of a new environment.

Conclusions and Future Directions

While expanding edge eco-evolutionary feedbacks are studied through invasions and climate shifts, these processes have fundamental differences that could produce drastically different results. Most of the models and case studies we have discussed involve the dynamics of single populations, potentially

overlooking interspecific interactions that may affect climate change outcomes. Although community-level climate change shifts have been widely studied, shifting edge phenotypes have generally not been considered. Since community-wide range shifts are challenging to study experimentally, more realistic modeling is essential to predict eco-evolutionary responses. Multiple models suggest that spatial sorting could play a substantial role in climate shifts, but this phenomenon has mainly been observed in biological invasions. It is possible that the additional effects of changing biotic and abiotic conditions may hinder this process in many cases. If there is high linkage between loci for adaptive and expansion traits, there may even be trade-offs between the two. If these trade-offs exist, we predict that populations under greater physiological stress due to novel biotic or abiotic conditions (as would be more commonly expected in climate change scenarios) will develop adaptive traits in favor of expansion traits. Quantitative genetic models investigating the interactions between local adaptation, spatial sorting, and allele surfing in expanding populations may help shed some light on these issues.

Although trait changes along expanding edges have been widely observed, the underlying mechanisms of the changes have been rarely studied. Many of our examples are at least partially due to plasticity, but the relative contributions of plastic versus genetic components are often unexplored. This deficit is mirrored in the theoretical literature. Plasticity can more rapidly facilitate the establishment of new populations than genetic changes alone (Robinson & Dukas, 1999). While plastic phenotypes may be genetically assimilated over time (Waddington, 1953; Pigliucci et al., 2006), this process could potentially be complicated by a shifting expansion front. Understanding the role of plasticity could be crucial for predicting the ultimate fate of edge-associated phenotypes.

Given the relevance of range expansions to global change biology, understanding the ecological and evolutionary processes at the leading edge will be critical for developing conservation and management responses. The inclusion of greater biological context into models such as life history trade-offs, biotic interactions, environmental conditions, and genetic mechanisms could provide better scenarios for considering the ephemerality or persistence of edge-associated traits.

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Appendix A

Table 1. Leading edge phenotypes by taxa

Documented leading-edge phenotypes by taxa and the underlying ecological drivers of range expansion. Non-bold taxa refer to animal species and bold taxa names refer to plant species. For ease of biological identification, animal taxa have been organized by class and plants (in bold) by family.

Taxa	Species name	Common name	Ecological driver	Trait category	Trait change in edge populations	Citation
Actinopterygii	*Coregonus albula*	vendace	Invasion	Morphology	Decreased body length	Amundsen *et al.* (2012)
				Metabolism	Faster growth rate	Bohn *et al.* (2004)
				Morphology	Decreased female gonad weight	Amundsen *et al.* (2012)
				Reproduction	Lower age of sexual maturity	
					Decreased fecundity	
	Hemichromis letourneuxi	African jewelfish	Invasion	Forage	Greater gut fullness	Lopez *et al.* (2012)
				Morphology	Better body condition	
					Higher gonadosomatic index	
	Neogobius melanostomus	round goby	Invasion	Forage	Greater gut fullness	Raby *et al.* (2010)
				Morphology	Increased male length	Gutowsky and Fox (2011)
					Increased female length	
				Metabolism	Higher resting metabolic rate	(Myles-Gonzalez *et al.*, 2015)
				Reproduction	Lower age to sexual maturity	MacInnis and Corkum (2000); Gutowsky and Fox (2012)
				Behavior	Higher gonadosomatic index	Gutowsky and Fox (2012)
					More aggressive	Groen *et al.* (2012)
					More dispersive	Myles-Gonzalez *et al.* (2015)
					Bolder	
	Siluris glanis	European catfish	Invasion	Morphology	Decreased body length	Carol *et al.* (2009)
					Better body condition	

Table 1 Continued

Taxa	Species name	Common name	Ecological driver	Trait category	Trait change in edge populations	Citation
Amphibia	*Rhinella marina*	cane toad	Invasion	Behavior	Faster range expansion rate	Phillips *et al.* (2006)
					Higher movement rate	Brown *et al.* (2007)
					Increased tendency to move	Alford *et al.* (2009)
					Greater movement endurance	Llewelyn *et al.* (2010)
				Morphology	Increased female and male tibia length	Phillips *et al.* (2006)
					Increased body length	Brown *et al.* (2013)
				Metabolism	Faster tadpole growth rate	Phillips (2009)
				Physiology	More neutrophils	Brown *et al.* (2015a)
					Higher phagocytosis rates	Brown *et al.* (2007)
					Higher spinal arthritis frequency	
Aves	*Estrilda astrild*	common waxbill	Invasion	Morphology	Redder breast pigmentation saturation in males	Cardoso *et al.* (2014)
					Reduced red face mask area in females	
	Limosa limosa islandica	Icelandic black-tailed godwit	Natural colonization	Morphology	Longer male bill length	Gunnarsson *et al.* (2012)
					Higher male bill/wing ratio	
	Passer domesticus	house sparrow	Invasion	Behavior	More exploratory of novel habitats	Liebl and Martin (2012)
					Faster consumption of novel foods	Liebl and Martin (2014)
						Liebl and Martin (2012)
				Physiology	Greater corticosterone response to stressors during breeding season	
					Reduced expression of stress hormone receptors	
	Sialis mexicana	western bluebird	Natural colonization	Behavior	Higher aggression score	Duckworth (2006)
					Lower social tendency	

Table 1 Continued

Taxa	Species name	Common name	Ecological driver	Trait category	Trait change in edge populations	Citation
Crustacea	*Pacifastacus leniusculus*	signal crayfish	Invasion	Morphology	Decreased male length	Hudina *et al.* (2012)
					Better body condition	Rebrina *et al.* (2015)
				Physiology	Better female hepatopancreatic state	
				Reproduction	Better female gonadal state	
	Uca pugnax	mud fiddler crab	Climate change	Metabolism	Faster developmental rate	Sanford *et al.* (2006)
Echinoidea	*Centrostephanus rodgersii*	longspine sea urchin	Climate change	Reproduction	Greater gonadosomatic index	Ling *et al.* (2008)
Gastropoda	*Acnthinucella spirata*	angular unicorn	Climate change	Morphology	Differences in relative height of shell spire	Hellberg *et al.* (2001)
Insecta	*Adelges tsugae*	hemlock woody adelgid	Climate change	Physiology	Greater cold resistance	Butin *et al.* (2005)
				Morphology	Higher wing aspect ratio	Hassall *et al.* (2009)
	Calopteryx splendens	banded demoiselle damselfly	Climate change		Greater flight ability in males	
				Morphology	Longer post-nodal section of the wing	Hassall *et al.* (2008)
	Coenagrion puella	azure damselfly	Climate change	Behavior	Increased juvenile activity	Therry *et al.* (2014a)
	Coenagrion scitulum	dainty damselfly	Climate change			Therry *et al.* (2014b; 2014c)
						Therry *et al.* (2014c)
						Therry *et al.* (2014c)
				Morphology	Increased flight muscle ratio	Therry *et al.* (2014c)
					Decreased wing loading	Therry *et al.* (2014b)
					Lower body fat	Therry *et al.* (2014b)
					Lower body mass	Therry *et al.* (2014b)

Table 1 Continued

Taxa	Species name	Common name	Ecological driver	Trait category	Trait change in edge populations	Citation
				Metabolism	Faster growth rate Decreased female larval development rate Decreased male larval development rate	Therry *et al.* (2014b)
				Physiology	Stronger encapsulation (immune) response Higher wing aspect ratio in males Faster flight speed	
	Erythromma najas	red-eyed damselfly	Climate change	Morphology	Faster developmental rate	Hassall *et al.* (2009)
	Harmonia axyridis	multicolored Asian lady beetle	Invasion	Metabolism	Lower queen/worker thorax volume ratio	Lombaert *et al.* (2014)
	Leptinotarsa decemlineata	Colorado potato beetle	Invasion	Metabolism	Greater thorax length	Lyytinen *et al.* (2009)
	Linepithema humile	Argentine ant	Invasion	Morphology		Abril *et al.* (2013)
	Merizodus soledadinus	ground beetle	Invasion	Morphology	Greater thorax width Greater femur length Greater interocular width Greater elytron length Greater body mass	Laparie *et al.* (2013)

Table 1 Continued

Taxa	Species name	Common name	Ecological driver	Trait category	Trait change in edge populations	Citation
	Melitaea cinxia	Glanville fritillary butterfly	Natural colonization	Metabolism	Higher flight metabolic rate	Haag *et al.* (2005)
	Pararge aegeria aegeria	speckled wood butterfly	Climate change	Morphology	Greater female and male thorax size Greater female and male mass Greater female and male abdomen	Hill *et al.* (1999)
				Reproduction	Larger clutch sizes	
	Polygonia c-album	Comma	Climate change	Morphology	Increased male thorax breadth	Braschler and Hill (2007)
Mammalia	*Castor fiber*	Eurasian beaver	Natural colonization	Life History	Younger age at dispersal	Hartman (1997b)
	Tamiasciurus hudsonicus	North American red squirrel	Natural colonization	Morphology	Larger cranial features	Goheen *et al.* (2003)
Nematoda	*Rhabdias pseudosphaero-cephala*	nematode lungworm	Natural colonization	Life History	Lower age of sexual maturity Larger female body size	Kelehear *et al.* (2012)
				Morphology	Larger larvae body size	
Reptilia	*Anolis sagrei*	brown anole	Invasion	Physiology	Decreased critical thermal minimum	Kolbe *et al.* (2014)
Asteraceae	*Mikania micrantha*	bitter vine	Invasion	Morphology	Decreased plume loading Decreased seed mass	(Huang *et al.*, 2015)
	Senecio inaequidens	South African ragwort	Invasion	Morphology	Larger pappus in diaspores	Monty and Mahy (2010)
	Senecio madagascariensis	Madagascar ragwort	Invasion	Morphology	Greater pappus volume	Bartle *et al.* (2013)
				Metabolism	Higher germination rates	

Table 1 Continued

Taxa	Species name	Common name	Ecological driver	Trait category	Trait change in edge populations	Citation
Caprifoliaceae	*Lonicera japonica*	Japanese honeysuckle	Invasion	Morphology	More branches	Kilkenny and Galloway (2013)
					Greater biomass	
				Life history	Higher survivorship	
Lythraceae	*Lythrum salicaria*	Purple loosestrife	Invasion	Reproduction	Smaller flowers	Colautti and Barrett (2013)
					Earlier flowering	
Pinaceae	*Pinus contorta*	Lodgepole pine	Natural colonization	Morphology	Decreased seed wing loading	Cwynar and MacDonald (1987)

Table 2. Cases without differences were found between edge and core

Non-bold taxa refer to animal species and bold taxa names refer to plant species. For ease of biological identification, animal taxa have been organized by class and plants (in bold) by family.

Taxa	Species name	Common	Ecological driver	Trait category	Trait description	Citation
Actinopterygii	*Coregonus albula*	vendace	Invasion	Reproduction	Mean egg size	Bøhn *et al*. (2004)
	Hemichromis letourneuxi	African jewelfish	Invasion	Behavior	Boldness Dispersal tendency	Lopez *et al.* (2012)
	Neogobius melanostomus	round goby	Invasion	Morphology	Body length	Brownscombe and Fox (2012)
				Behavior	Activity Boldness	Groen *et al.* (2012)
Amphibia	*Rhinella marina*	cane toad	Invasion	Dispersal	Dispersal speed Directional dispersal	Llewelyn *et al.* (2010) Brown *et al.* (2015b)
Aves	*Sturnus vulgaris*	European starling	Invasion	Morphology	Wing length Wing pointiness	Bitton and Graham (2015)
	Estrilda astrild	common waxbill	Invasion	Morphology	Breast pigmentation in females Red mask area on face in males Red bill saturation in both sexes Red breast area in both sexes	Cardoso *et al.* (2014)
	Passer domesticus	house sparrow	Invasion	Behavior	Latency to touch novel objects Behavioral flexibility	Liebl and Martin (2014)
Insecta	*Atalopedes campestris*	sachem skipper	Climate change	Physiology	Critical thermal minimum	Crozier (2003)
	Coenagrion scitulum	dainty damselfly	Climate change	Physiology	Adult activity	Therry *et al.* (2014a)
					Phenoloxidase activity (immune function) in females	Therry *et al.* (2014c)

Table 2 Continued

Taxa	Species name	Common	Ecological driver	Trait category	Trait description	Citation
	Leptinotarsa decemlineata	Colorado potato beetle	Invasion	Life history Morphology Dispersal	Larvae-to-adult mortality rate Overwintering mortality rate Adult weight Body mass	Lyytinen et al. (2009)
	Linepithema humile	Argentine ant	Invasion Climate change	Morphology Reproduction	Fat content in queens Worker thorax volume Oviposition rate	Abril *et al.* (2013) Hill et al. (1999)
	Pararge aegeria tircis	Speckled wood butterfly			Aspect ratio Wing loading	
Echinoidea	*Centrostephanus rodgersii*	longspine sea urchin	Climate change	Physiology Reproduction	Thermal tolerance Reproductive phenology	Ling *et al.* (2008)
Asteraceae	*Mikania micrantha*	bitter vine	Invasion	Morphology	Pappus radius	Huang *et al.* (2015)
	Senecio madagascariensis	Madagascar ragwort	Invasion	Morphology	Achene size	Bartle *et al.* (2013)

Table 3. Trade-offs associated with edge phenotypes

Taxa	Species	Common name	Edge trait	Trade-off	Citation
Actinopterygii	*Coregonus albula*	vendace	Faster sexual maturation	Shorter body length Shorter life span	Bøhn *et al*. (2004) Amundsen *et al.* (2012)
Amphibia	*Rhinella marina*	cane toad	Increased leg length Faster growth	Increased rates of spinal arthritis Reduced immune function	Brown *et al.* (2007)
Aves	*Sialis mexicana*	western bluebird	Increased aggression	Lower fecundity	Duckworth (2006)
	Limosa limosa islandica	Icelandic black-tailed godwit	Increased male size	Lower breeding success	Gunnarsson *et al.* (2012)
Insecta	*Conocephalus discolor*	bush cricket	Increased flight ability and endurance	Lower egg production	Simmons and Thomas (2004)
	Melitaea cinxia	Glanville fritillary	Earlier sexual maturation	Shorter lifespan	Hanski *et al.* (2006)
	Pararge aegeria	speckled wood butterfly	Larger egg clutch size Increased flight ability	Lower fecundity	Hughes *et al.* (2003)
Nematoda	*Rhabdias pseudosphaerocephala*	nematode lungworm	Larger egg size	Lower fecundity	Kelehear *et al.* (2012)

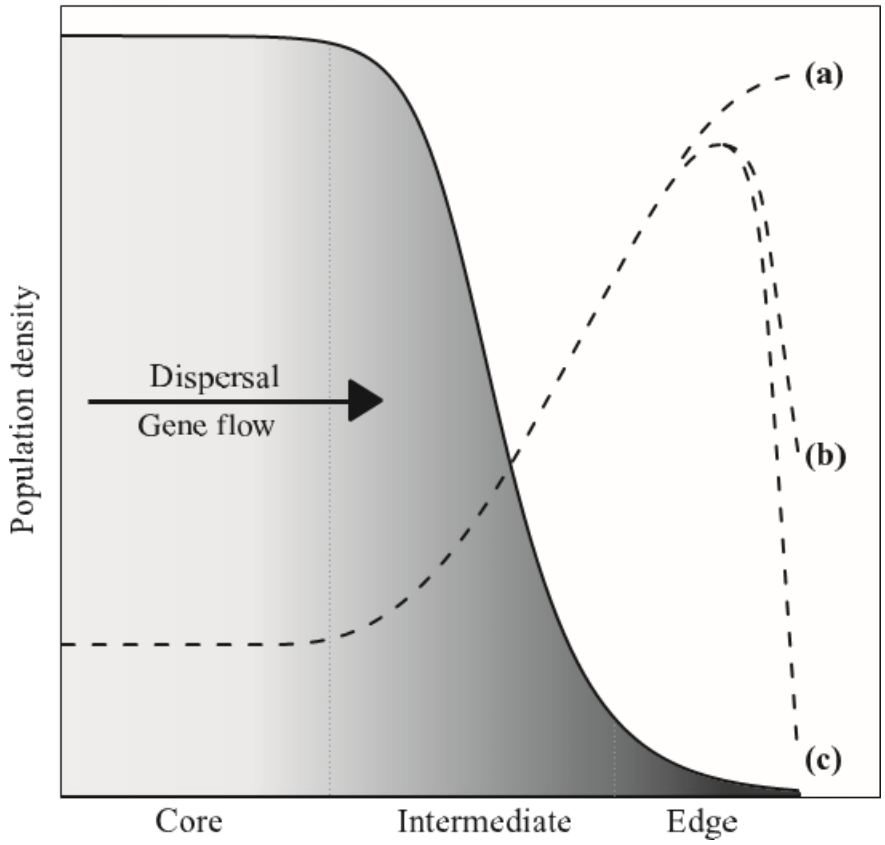

Figure 1. Range expansion demographics

As the population transitions from core to edge, density (solid line) decreases. Reproductive rate (dashed line) increases near the edge A), but is reduced at the range front in populations subject to weak B) or strong C) Allee effects.

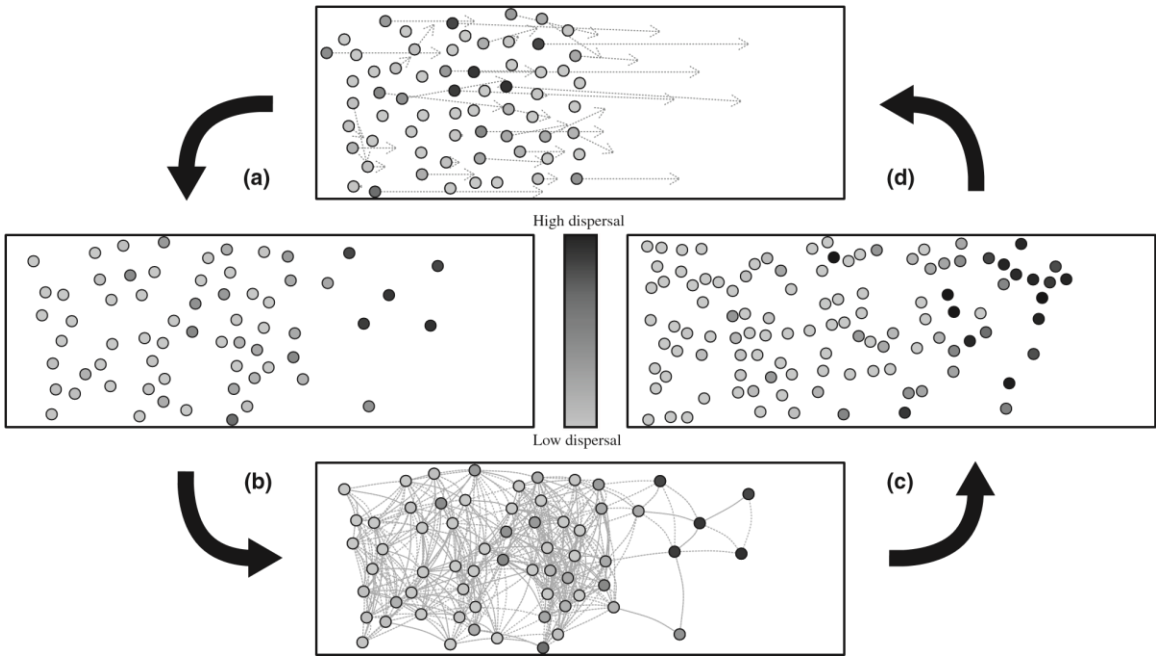

Figure 2. Spatial sorting and the Olympic Village effect

A) When a population with dispersal variation expands, individuals with a higher dispersal ability will be able to travel farther from the core. B) Olympic Village effect: Individuals at the edge are limited to mating with neighbors, many of whom are highly dispersive. C) If dispersal is heritable, the offspring at the edge will be better dispersers than the ones at the core. D) The offspring disperse and the cycle repeats.

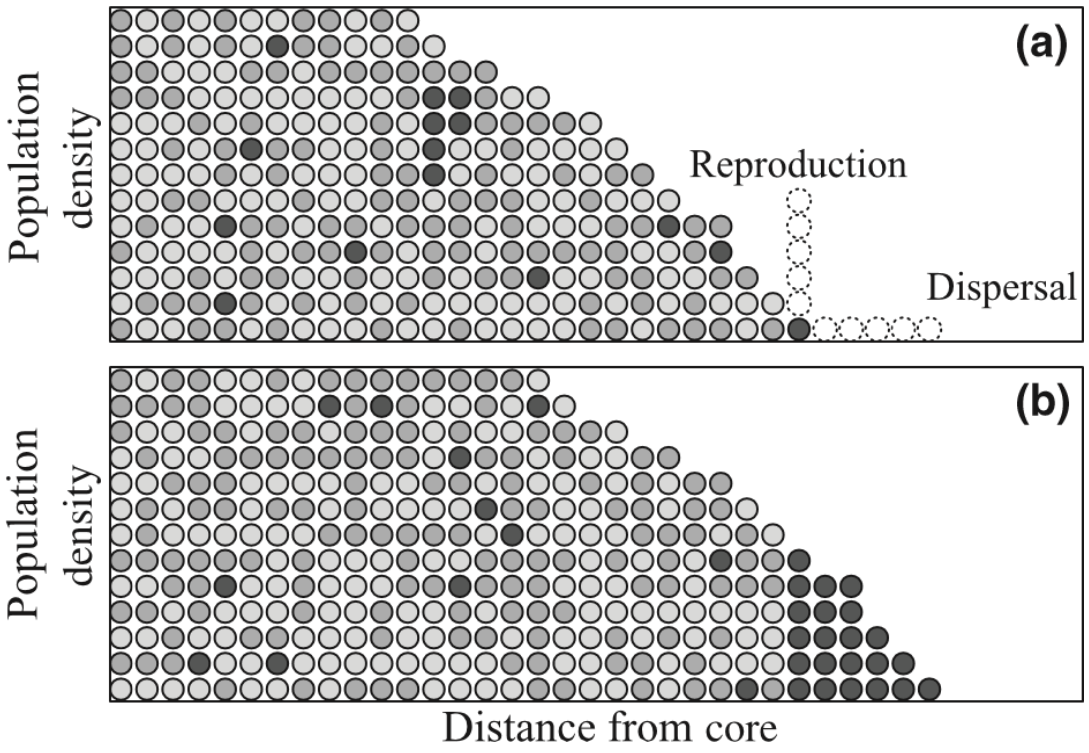

Figure 3. Allele surfing

The expansion front undergoes serial founder effects; A) edge alleles that are rare in the overall population (dark dots) can B) become fixed in newly colonized areas through reproduction and dispersal. This process can happen regardless of the allele's phenotypic effect. Each column represents a deme with allele frequencies proportional to its colored dots.

CHAPTER II
PERSONALITY SHIFTS ALONG THE NON-NATIVE RANGE EXPANSION GRADIENTS OF AN ORBWEAVER SPIDER

Abstract

Successful biological invasions are characterized by the spread of a population across a landscape. Range expansion conditions can favor different phenotypes at the leading edges of the range compared to those at the core. *Cyrtophora citricola* is a non-native spider in Florida that has rapidly and independently spread along both eastern and western coasts from a common origin. Personality traits mediate how individuals interact with their environment, and some types may fare better in colonization contexts. In this study, we asked whether the leading edges of these two range expansions are composed of different personality types compared to the core and whether range-level patterns in personality are consistent between two populations expanding from the same core. We predicted that more aggressive, more active, more exploratory, and bolder spiders would be at the leading edge, because these traits can facilitate colonization or are associated with neophilia. While we found that leading-edge spiders were indeed faster to attack prey stimuli and more active in novel environments, the two populations diverged in risk-taking behaviors. Western spiders were increasingly shy and less exploratory at newer colonization sites, whereas eastern spiders were bolder at newer sites. The divergence in exploratory behavior and boldness between these populations highlights the difficulties in making generalizations on how traits may become assorted across an expanding range and stress the importance of using replicate populations when possible. These results suggest that range-level processes are either inconsistent or that the strength of local adaptation may swamp processes such as spatial sorting.

Introduction

Invasions are characterized by non-native species establishing and expanding their ranges against potential novel ecological and evolutionary pressures (Sakai et al. 2001). Because some invasive species pose threats to native populations, communities, and ecosystems (Simberloff et al. 2013), it is important to understand the processes underlying range expansions, as this knowledge can help us determine the rate of spread and the characteristics of the invading front (Phillips et al. 2010b). This information has implications for management strategies of the invasive species as well as native species conservation (Travis and Park 2004, Carere and Gherardi 2013, Shine 2017).

A species' expanding range comprises three components- the core, intermediate, and leading edge. The area of initial introduction often functions as the core of the population, with population density ranging from highest at the core to lowest at the edges (Phillips 2009, Phillips et al. 2010b) (Figure 4). The dynamics of spreading populations can create demographic and phenotypic

clines across their ranges (Hallatschek and Nelson 2008, Shine et al. 2011). Better dispersers are thought to be disproportionately represented at the leading edges of expansion, owing to spatial sorting (Shine et al. 2011). Invasive cane toads (*Rhinella marina*) from Australia are a classic example of this phenomenon. Toads at the leading edge of invasion have longer legs (Phillips et al. 2006), grow faster as juveniles (Phillips 2009), and move in longer and straighter trajectories (Alford et al. 2009, Lindstroem et al. 2013) compared to toads in the core population. Since species ranges are constrained by unfavorable abiotic and biotic conditions, phenotypes at the edge might be more adept colonizers of novel environments owing to faster reproduction or increased tolerance to extreme conditions (Amundsen et al. 2012, Kolbe et al. 2014)

As a relatively labile trait, behavior allows individuals to respond rapidly to new environments and situations (Houston and McNamara 1999). Behavior may be temporally and contextually consistent on an individual level and different behaviors are often intercorrelated, commonly referred to as personalities and behavioral syndromes (Gosling 2001, Sih et al. 2004, Bell et al. 2009). A wide variety of taxa, including spiders, exhibit repeatable responses in behavioral traits relating to boldness, exploration, activity, and aggressiveness (Tulley and Huntingford 1988, Mather and Anderson 1993, Riechert and Hedrick 1993, Dingemanse et al. 2002). Populations comprise different personality types, each with varying ecological impacts (Sih et al. 2012); for example, bolder and more aggressive individuals can have more agonistic interactions within their communities (Duckworth and Badyaev 2007, Pruitt et al. 2012).

Personality traits influence life history traits relevant to invasions, including dispersal, growth, and reproduction. Bolder, more aggressive, more active, and more exploratory individuals are often more dispersive (Fraser et al. 2001, Rehage and Sih 2004, Duckworth and Badyaev 2007, Cote et al. 2010b). Therefore, dispersive individuals with particular personality types might be more prevalent at the leading edges of their range expansion (Clobert et al. 2009). Individual dispersal can affect overall population spread, including increasing the rate of range expansion (Phillips et al. 2010a, Perkins et al. 2013).

Although there is growing agreement that leading edge individuals of range expansions can differ phenotypically from those at the core (Bohn et al. 2004, Shine et al. 2011, Chuang and Peterson 2016), less is known about how predictable these patterns are. Many studies follow range expansions possessing a single wave front (Phillips et al. 2006, Duckworth and Badyaev 2007, Gunnarsson et al. 2012, Liebl and Martin 2012). These documented patterns of range-level shifts form important case studies of range expansions. However, studies with multiple range expansion fronts can help us determine how consistent patterns of phenotypic change are in the same system and what

factors might underlie the observed differences. For instance, Gutowsky and Fox found longer round goby fish (*Neogobius melanostomus*) at both expanding fronts upstream and downstream of the population core (2011). Consistent findings at leading edges support the idea that the process of range expansion itself can produce predictable phenotypic and life history shifts. In contrast, differing patterns in replicate range expansions can reflect environmental conditions exerting stronger pressures than range expansion processes.

In this study, we examined whether personality types of the tentweb orbweaver, *Cyrtophora citricola* (Forskål 1775), varied clinally across its expansion gradients in its non-native Florida range. We observed two replicate populations spreading northward from a common origin along opposite coasts to address the following questions in this study: 1) Which behavioral responses, if any, constitute repeatable personality traits? 2) Are any behavioral traits intercorrelated with each other? 3) Do individuals at the core and leading edges differ in mean personality scores? 4) Are range-level phenotypic patterns consistent across the two replicate expansion fronts sharing a common origin? Our hypothesis is that traits such as greater aggression, greater exploratory behavior, higher activity levels, and higher boldness are found at leading edges because these personality types are often associated with dispersal. We predicted that leading-edge spiders would exhibit greater boldness, activity, exploration, and aggression and that these behavior traits would be repeatable with intercorrelations exhibited among them. We also predicted that, owing to similar range expansion processes underlying trait shift and spatial selection, the two replicate populations would show similar patterns of behavioral variation across their expansion gradient. Alternatively, if different behavioral patterns occur across replicate range expansions, this would suggest that local selective pressures play a greater role in shaping populations than do range expansion processes like personality-linked dispersal or colonization.

Methods

Study organism and introduction history

Cyrtophora citricola is a facultatively colonial spider that can reside in colonies made up of large networks of individual capture webs linked by shared framework threads (Wheeler 1926, Lubin 1974, Leborgne et al. 1998). It does not exhibit behaviors characteristic of social spider species (i.e., cooperatively foraging, engaging in parental care, or splitting colony tasks), but nonetheless forms persistent aggregations (Lubin 1980).

This species is native to the Mediterranean, Middle East, Asia, and Africa (Forskål 1775, Kullmann 1958, 1959). In recent years it has been repeatedly introduced into the Americas and the Caribbean (Florez Daza 1996, Alayon

Garcia et al. 2001, Alayon Garcia 2003, Alvares and De Maria 2004, Starr 2005, Viquez 2007). It was first observed in Florida, USA around 2000. The first survey of this spider was conducted between 2002 – 2004 and concluded that *C. citricola*'s range was restricted to the city limits of Homestead (Edwards 2006). Given the conspicuousness of *C. citricola*'s webs and this initial survey, we assume that Homestead is where *C. citricola* was initially established and began spreading from. Therefore, we treated Homestead as the population core of its non-native range in Florida.

Given its proclivity for sturdy substrates in open habitats (Madrigal Brenes 2012, Chuang and Leppanen 2018), *C. citricola* largely frequents urban and residential areas on the east and west coasts of Florida. Its webs are found on a broad variety of plant species, as well as on manmade structures, including guard rails, bridge railings, fences, and street signs.

We completed our first surveys of *C. citricola* populations in southern Florida in May 2014 and March 2015 to determine the range limits of *C. citricola* in the state. We noted that *C. citricola* had a northern range edge at latitude 27.451118 (Fort Pierce, FL) on the east coast and latitude 27.816869 (St. Petersburg, FL) on the west coast. Our subsequent surveys in January 2015, March 2015, July 2015, and August 2017 have shown that *C. citricola* has extended its northern range limit each year of our surveys, leading us to assume that this spider's range is primarily expanding on the northern front. As of August 2017, we observed *C. citricola* colonies appearing as far north as Vero Beach (27.7156856, -80.4694739) and Palm Harbor (28.12911484, -82.73988883) on the eastern and western coasts, respectively (Figure 5). We assume that expansion has occurred gradually northward and latitude can function as a proxy for its colonization history, although longer distance dispersal events leading to earlier colonization at northern sites are also possible. Online photo and locality records of this species on BugGuide.net also show more northward sightings at later dates, although there are few overall sightings.

Field data

We scored the behavior of individuals from the following populations on the east coast of Florida in July of 2015: Ft. Lauderdale (26.1412497), West Palm Beach (26.7420741), Ft. Pierce (27.4294654), and Vero Beach (27.645231). We scored individuals from the following west coast populations in July of 2017: Naples (26.1449798), Sarasota (27.335939), Ft. Myers (26.6187703), and Clearwater/Palm Harbor (28.12911484) in July 2017 (Figure 5).

In total we measured the behavior of 1,224 individuals of all size and age classes: 282 from the core, 558 from the western population, and 384 from the eastern population. We collected data from between three to five sites in each of the cities along the range. At each site, we censused four to eight colonies and

between four and thirty individuals per colony. The number of colonies and number of individuals scored depended on the number of accessible colonies present and the size of these colonies. Most of the individuals scored were located on guard rails, bridge railings, and citrus trees, where the height and structure of the web substrate did not impede our use of web-vibrating equipment meant to stimulate aggressive behaviors.

Behavioral assays

The behavioral methods described below are adapted from standard assays of spider behavior (Riechert and Hedrick 1993, Pruitt et al. 2008, Kralj-Fiser and Schneider 2012, Grinsted et al. 2013, Keiser and Pruitt 2014). The test for aggressiveness towards prey was performed *in situ* prior to our collecting the individual. Subsequent tests for boldness towards predatory cues, exploration tendency, and activity were completed in an indoor setting to control for environmental factors that tend to vary, such as wind speed. These latter behavioral assays were performed within five hours of capture.

Aggressiveness towards prey

A variety of different artificial web vibrators have been used to mimic prey trapped in webs, in order to elicit attack responses in spiders (Frohlich and Buskirk 1982). Prey vibrations range in frequency between 50 to 1000 Hz, encompassing insects such as flies, bees, moths, and leafhoppers (Suter 1978, Burgess 1979). When insect prey struggle in webs, their vibrational frequency can become irregular and drop to 50 Hz or below. We measured individual responses to vibrations produced by an electric gum stimulator (BrushPoint Vital Health Power Oral-B Care System). We used a laser vibrometer (Polytec PDV100) to quantify its vibrational frequency, which ranged from 45 to 50 Hz.

We measured the latency of an individual to attack the rubber tip of the vibrating stimulus. We applied the gum stimulator to the edge of each web, a distance from the spider that ranged from 3 to 25 cm depending on the size of the spider. We recorded whether the individual responded to the stimulus, whether an attack had been completed (defined by a bite on the rubber tip of the stimulator), the latency to react to vibrations, and the latency to mount a full attack on the gum stimulator in seconds. Common reactions to the stimuli prior to an attack included orienting towards the source of disturbance, plucking or shaking the web, retreating away from the stimulus. The total duration of the attack response was calculated as the difference between the response and attack latency.

Exploration/Activity

We placed a test subject into an empty plastic container (150 mm x 65 mm Petri dish) and allowed it to explore this novel space freely. Exploratory activity was defined as any behaviors that involved displacement of an individual,

including walking along the bottom of the container, climbing on the walls, and initiating web-building activities. All of these activities entailed the individual laying down silk. The trials continued as long as the spider was active and ended once the individual had ceased activity for five minutes. We recorded whether exploration was initiated within the trial period, the latency to initiate activity, the number of exploratory activity bouts exhibited, and the total amount of time spent exploring in seconds.

Boldness

We measured an individual's propensity to engage in risky behaviors in a novel environment. This test occurred in the same 150 mm x 65 mm Petri dish after completion of the Exploration/Activity trial. After the spider had ceased exploration for five consecutive minutes, we used a nasal aspirator to deliver two quick puffs of air from 3 cm away. This sensation simulates the aerial approach of an avian predator (Riechert and Hedrick 1993, Pruitt et al. 2011). All individuals exhibited a huddled defensive posture in response to these puffs. We subsequently recorded whether an individual resumed activity within the trial period, which usually included walking and web-building activities, and the latency to do so. The trial ended after 3600s if the spider had not resumed activity within that period.

Common garden experiment

We collected egg sacs from each site in Florida, placing each one in a different 2 oz polypropylene container with a clear polyethylene lid. We brought these into our laboratory at The University of Tennessee, where egg sac maintenance consisted of weekly misting with water until spiderlings emerged. We separated the emerging spiderlings into groups of five siblings per 2 oz cup to promote survivorship, since early instars were observed sharing prey (Chuang, personal observation). Every two to three days, we offered size-matched crickets (ranging from one to two week-old *Acheta domesticus*), fruit flies (*Drosophila melanogaster*), or termites (*Reticulitermes* sp.) *ad libitum* to each group of siblings and misted their container. As individuals reached the third instar post-emergence, we separated them into individual containers to reduce cannibalism. Once each individual had established a capture web in its new container and had been fed twice, we conducted assays for aggressiveness towards prey, exploration/activity, and boldness towards predatory cues. To calculate repeatability of each behavior, we repeated each of these assays twice more over three to four weeks; repeatability estimates are not known to change significantly with more observations (Bell et al. 2009).

Statistical methods

We analyzed all data in R (R Core Team 2019). We tested behavioral measurements from the common garden-reared individuals in the 'rptR' package

in R with Poisson distributions to estimate repeatability (Pruitt et al. 2008, Stoffel et al. 2017). Repeatability estimates the proportion of behavioral variation at the group level that can be attributed to variation among individuals compared to variation within individuals (Boake 1989, Hayes and Jenkins 1997, Bell et al. 2009). A high repeatability score indicates that behavioral variance at the group level is higher than variance at the individual level, as might be expected if individuals consistently differ from one another in their behaviors. We subsequently used the following five behavioral measurements that showed significant repeatability to answer our questions about personality shifts across expansion gradients: latency to attack prey, prey attack duration, latency to explore, duration of total activity, and latency to resume activity after a predatory stimulus.

We applied Spearman's rank correlation tests to these five measured behaviors from the field to test for evidence of behavioral syndromes. In addition, we tested each population separately to determine whether trait correlations have diverged among populations. To avoid spurious correlative results, we applied the Benjamini-Hochberg procedure to resulting p-values. This method uses a sequential modified Bonferroni correction and tests multiple hypotheses to reduce chances of Type I errors (Benjamini and Hochberg 1995).

We used logistic regression models with a binomial logit link function to determine whether population was a significant predictor in the frequency of spiders engaging in our behaviors of interest– namely, responding to a prey stimulus, completing an attack, initiating exploration, or resuming activity after a predatory stimulus. We used negative binomial regression models to determine whether population was a significant predictor in individual latency or duration to perform these behaviors. Confounding variables such as length and sex were included as predictors in the full models. We used Tukey's HSD tests to test for pairwise differences between each population's behavioral responses.

We used separate models for each population to determine whether latitude (a proxy for distance from the core) significantly predicted of each behavior, and length and sex were included. For model selection, we used the stepAIC function in R package *MASS* to create a final model through both forward and backward stepwise regression (Ripley and Venables 2002). Forward selection involves starting with no predictors and subsequently adding predictors that contribute the most towards explaining the data. Backward selection begins with the full model and iteratively removes predictors that explain the data the least.

Results

Repeatability of behavioral traits

Most of the behaviors tested showed moderate repeatabilities (r = between 0.22 and 0.38). (Table 4). Activity bout frequency showed overlap in its 95% confidence interval with 0 (r = 0.220, n = 67, 95% CI = [0, 0.322]), so we did not consider it to be a repeatable trait and did not compare it with other behaviors in subsequent analyses.

Behavioral syndromes

When comparing behaviors from all individuals, we found a few existing intra- and inter- correlations between behaviors (Table 5). For example, individuals that responded more quickly to the prey stimulus generally took longer to attack prey (ρ = -0.384, n = 1223, p < 0.0001), and individuals that were slower to begin exploring a novel environment tended to explore longer (ρ = -0.238, n = 1223, p < 0.0001). However, the latency to explore was positively correlated not only to the duration of an attack (ρ = 0.112, n = 1223, p < 0.0001), but also to the latency to resume activity (ρ = 0.132, n = 1223, p < 0.0001).

However, the species-level trait correlations were not equally found in each population (Table 5). For instance, the eastern population did not show a correlation between prey attack duration and latency to explore (ρ = 0.066, n = 384, p = 0.297), but spiders there uniquely showed a slight positive correlation between latency to respond to prey and latency to explore (ρ = 0.132, n = 384, p < 0.0001). The western population was the only population that exhibited the attack-exploration correlation (ρ = 0.111, n = 557, p = 0.009).

Population differences in behavior from spiders in the field

We found that population was a significant predictor in all of the logistic regression and negative binomial regression models besides response frequency (Table 6, Table 7). According to our Tukey's HSD tests, both eastern ($\bar{x}$ = 0.1224, 95% CI = (0.0321, 0.2126), p = 0.0043) and western ($\bar{x}$ = 0.1593, 95% CI = (0.0755, 0.2431), p < 0.0001) spiders had higher attack frequencies than those of the core. Patterns of population-level differences in exploratory tendency and boldness were similar, in that western spiders were less likely to explore compared to eastern ($\bar{x}$ = -0.3787, 95% CI = (-0.4542, -0.3033), p < 0.0001) and core spiders ($\bar{x}$ = -0.2065, 95% CI = (-0.2864, -0.1266), p < 0.0001). Western spiders were also less likely to resume activity compared to eastern ($\bar{x}$ = -0.2147, 95% CI = (-0.2849, -0.1445), p < 0.0001) and core spiders ($\bar{x}$ = -0.1408, 95% CI = (-0.2154, -0.0662), p < 0.0001).

We also detected population-level differences among the spiders that displayed the behaviors of interest (i.e. responding, attacking, exploring, resuming activity) (Table 7, Figure 6). The eastern and western populations were

faster to respond to prey stimuli compared to the core ($\bar{x}$ = -0.6413, 95% CI = (-0.9937, -0.2889), $p < 0.0001$; $\bar{x}$ = -1.0286, 95% CI = (-1.3633, -0.6939), $p < 0.0001$). Eastern and western spiders were also faster to complete an attack compared to core spiders, respectively ($\bar{x}$ = -0.6317, 95% CI = (-1.0166, -0.2468), $p < 0.0001$; $\bar{x}$ = -0.4201, 95% CI = (-0.0556, -0.7846), $p < 0.0001$). For the exploration and boldness assays, the western population significantly differed from the core and eastern population. Western spiders were generally slower to explore compared to core ($\bar{x}$ = 0.9911, 95% CI = (0.4991, 1.4832), $p < 0.0001$) and eastern spiders ($\bar{x}$ = 1.2260, 95% CI = (0.7842, 1.6677), $p < 0.0001$). Core and eastern spiders were also bolder than western spiders, with faster latencies to resume activity after a predatory cue ($\bar{x}$ = -0.4594, 95% CI = (-0.9301, 0.0113), $p < 0.0001$; $\bar{x}$ = -0.5586, 95% CI = (-0.9709, -0.1464), $p < 0.0001$).

Latitudinal clines in behavior

Our individual models for the western and eastern populations showed that some behaviors varied with latitude, a proxy for the distance from the core population and colonization history (Table 8, Table 9). Namely, western spiders had shorter attack sequences ($Z = -3.780$, $n = 265$, $p = 0.0002$) and were active longer ($Z = 1.964$, $n = 244$, $p = 0.049$) at increasing latitudes. Eastern spiders not only had shorter attack sequences ($Z = 2.344$, $n = 166$, $p = 0.019$) but were also slower to explore ($Z = 3.221$, $n = 270$, $p = 0.001$), active for longer ($Z = 3.110$, $n = 270$, $p = 0.002$), and faster to resume activity after a predatory stimulus ($Z = -2.514$, $n = 286$, $p = 0.012$) at increasing latitudes.

Body length and sex often influenced behavior as well. Larger spiders were slightly more likely to respond to prey stimuli ($Z = -2.502$, $n = 1092$, $p = 0.012$). They also took marginally longer to attack prey stimuli ($Z = 2.583$, $n = 520$, $p = 0.010$) and were slower to begin exploration ($Z = -1.958$, $n = 693$, $p = 0.050$).

Discussion

This is the first report of the non-native range expansion of *Cyrtophora citricola* in Florida, with particular reference to aspects of personality and behavioral syndromes. Since its discovery in 2000, *C. citricola* has expanded its range about 280 and 350 km northward along its respective eastern and western coasts of southern Florida. As of August 2017, its northern range extent occurs in Vero Beach (27.6806831,-80.4633822) and Palm Harbor (28.1148801,-82.768991) on the eastern and western coasts (Figure 5).

We found that *C. citricola* does indeed show repeatability in most behavioral traits, suggesting that individuals exhibit stable responses. The repeatability scores ranging between 0.22 and 0.38 are moderate but very consistent with values found in the personality literature. For example, in Bell et

al.'s meta-analysis of repeatability studies, the average repeatability in over 750 estimates of behaviors of 98 species was 0.37 (2009). Repeatability in many of our tested traits has also been demonstrated in other spider species, such as latency to attack (*Agelenopsis aperta* (Hedrick and Riechert 1989); *Dolomedes triton* (Johnson and Sih 2007); *Larinioides sclopetarius* (Kralj-Fiser and Schneider 2012); *Nephilengys livida* (Kralj-Fiser et al. 2012)), latency to emerge after a predator stimulus (*Agelenopsis aperta* (Riechert and Hedrick 1990); *Dolomedes triton* (Johnson and Sih 2007); *Larinioides sclopetarius* (Kralj-Fiser and Schneider 2012); various *Anelosimus* species (Pruitt et al. 2011)), latency to explore a novel environment (*Agelenopsis riechertae* (Bosco et al. 2017)), and total activity (*Eris militaris* (Royaute et al. 2014)). Thus, we interpreted among-individual variation in behavioral scores as different personality types present in *C. citricola*.

Notably, we detected behavioral clines along the two range expansions, leading to different personality compositions at the leading edges and core of *C. citricola*'s Florida range. Spiders from more newly colonized sites attacked prey faster and were more likely to complete an attack, indicating higher levels of aggression towards prey. Leading-edge spiders were also more active, exploring novel test arenas longer than their core counterparts. Eastern spiders alone were bolder towards their expansion front.

These results in part support our initial predictions that more aggressive, active, and bolder personality types might be more prevalent at the expansion front, since these traits may promote colonization. Exploratory tendencies such as greater activity are expected to be more common at range edges than at the core, because more active individuals might find shelter more easily (Cote et al. 2010a, Cote et al. 2010b, Chapple et al. 2012, Sih et al. 2012) or benefit from feeding opportunities under lower conspecific densities (Brown et al. 2013, Gruber et al. 2017a). Exploring physical surroundings provides orbweavers with important information for making web-building decisions (Vollrath 1992). Since web-site location influences sun exposure, prey availability, disturbance frequency, and conspicuousness for predators, a willingness to explore a habitat more thoroughly can allow individuals to find and settle in higher quality sites.

Aggression is also a behavioral trait posited to contribute to successful range expansion (Holway and Suarez 1999, Weis 2010, Chapple et al. 2012, Hudina et al. 2014). The success of western bluebirds (*Sialia mexicana*) recolonizing their historic natural range has been attributed to the expansion front composed of more dispersive, aggressive males capable of outcompeting congeners for nesting sites (Duckworth and Badyaev 2007). While we documented faster attacking spiders at the edge, this behavior can nonetheless aid in successful colonization at sites if higher prey-capture rates lead to higher

survival or reproductive rates. Since *Cyrtophora* spiders weave non-sticky webs (Lubin 1973), prey are often entangled by intersecting silk strands without adhering to them directly, allowing prey to escape if spiders do not respond and attack quickly enough. Faster attack responses in spiders can be associated with higher prey capture rates (Costa-Pereira and Pruitt 2019), which can improve survival rates and increase reproductive efforts at the leading edges of range expansions.

The observed behavioral clines may also reflect environmental factors such as predator density, prey availability, habitat characteristics, and climatic factors occurring across the expansion gradient (Gruber et al. 2017b). *Cyrtophora citricola*'s range expansion follows a latitudinal gradient of over two degrees Celsius. While most studies demonstrating latitudinal changes in behavior take place over much greater scales (Laurila et al. 2008, Maldonado et al. 2012, Diaz et al. 2013), climatic differences between the leading edges (Palm Harbor, Vero Beach) and the core (Homestead) do exist. Homestead is ~2°C warmer year round, and experiences ~25 cm more rain in the summer, whereas Vero Beach and Palm Harbor are rainier in the winter (Florida Climate Center, 2019). These differences can translate into different abiotic conditions and biotic communities with different selection pressures for each population.

Spatial sorting can also explain behavioral clines that exist across expansion gradients (Shine et al. 2011). Spatial sorting occurs in expanding populations when dispersive phenotypes disperse further from their natal environments than nondispersers. If dispersal tendency is linked to other behaviors such as aggression, boldness, exploration, and activity in *C. citricola*, this can explain why some personality types exhibit an expansion gradient. Specifically, if aggression and activity is linked to dispersal, this would suggest that spatial sorting of the same behaviors had occurred twice independently, given our observed patterns.

The boldness-exploration syndrome was a consistent trait correlation found in all three populations. This syndrome has been documented previously in other systems (Fraser et al. 2001, van Oers et al. 2004, Kortet and Hedrick 2007, Wilson et al. 2009, Cote et al. 2010b, Wisenden et al. 2011, Mazue et al. 2015). This linkage in *C. citricola* supports the idea that spiders from the western and eastern populations have diverged in their responses to novel, risky situations. The discovery that spiders from the western population exhibit decreasing boldness towards newer colonization sites runs contrary to expectations. Individuals with higher exploratory and risk-taking behaviors are usually observed at expanding front edges (Liebl and Martin 2012, Myles-Gonzalez et al. 2015, Gruber et al. 2017a). These traits may be linked to dispersal and a general willingness to move outside of a familiar natal environment (Cote et al. 2010a),

which are traits that are likely to become spatially assorted. Higher exploration and boldness may also be favored by selection if the costs associated with these behaviors are lower at range edges. These lower costs could be due to lower conspecific density, resulting in lower transmission of parasites and conspicuousness to predators, or simply because the biotic community has not had time to respond to new available hosts or prey yet. Since spiders from populations with weaker predation pressure are often bolder (Riechert and Hedrick 1990), it is possible spiders in the eastern population are under lower predation pressure compared to the shyer, risk-averse western spiders.

The mechanisms underlying these phenotypic shifts in expanding ranges are not well understood. However, the patterns in *C. citricola* suggest a few possibilities: 1) that spatial sorting tends to occur in expanding populations, but that the directionality of risk-taking phenotype shift is unpredictable and random; 2) that the strength of trait selection is greater than spatial sorting in at least one population and has resulted in opposite patterns; 3) these traits solely represent local adaptation to differing environmental pressures present along both coasts. 4) We also cannot rule out that these patterns may be the result of random, non-adaptive processes. Thus, we recommend further studies investigating whether higher dispersal in *C. citricola* is correlated with the personality types we documented at the leading edges to determine whether spatial sorting is occurring in one or both populations.

Conclusion

We studied two populations of *C. citricola* independently expanding from a single origin to determine whether patterns of phenotype shifts across the range occur consistently. We found progressively more active and aggressive spiders at newer sites towards the leading edges of range expansion, suggestive that range expansion processes result in some repeatable patterns. However, risk-taking behaviors like exploration and boldness actually exhibited opposite patterns from the core to the leading edges, highlighting our lack of understanding of how range expansion processes work to shape phenotypic composition as well as how they might interact with selection pressures from each site. These patterns further emphasize the challenges of reliably predicting range expansions and the need to examine these processes from a mechanistic standpoint.

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Appendix B

Table 4. Repeatability estimates for assayed behaviors

Repeatability estimates of 66 common garden spiders assayed 3 times over 3-4 months, where all behaviors except the frequency of tiptoes exhibited statistically significant correlation coefficients. Given the overlap in values with 0, the frequency of activity bouts are not considered repeatable. The name of the behavioral assay is bolded.

Behavioral Assays	R	SE	95% CI	p-value
Activity/Exploration				
Latency to explore in a novel environment (s)	**0.295**	0.085	(0.084-0.421)	1.20×10^{-4}
Frequency of activity bouts	**0.220**	0.083	(0-0.322)	1.45×10^{-4}
Total activity duration (s)	**0.341**	0.084	(0.138-0.400)	1.97×10^{-5}
Boldness Assay				
Latency to resume activity after predator stimulus (s)	**0.272**	0.080	(0.075-0.386)	1.46×10^{-4}
Aggression Assay				
Prey Attack Duration (s)	**0.342**	0.094	(0.135-0.457)	2.63×10^{-5}
Latency to respond to prey stimulus (s)	**0.346**	0.107	(0.071-0.493)	5.72×10^{-5}

Table 5. Pairwise comparisons between behaviors

Spearman's ρ pairwise comparisons between behavioral variables measuring exploration/activity, foraging aggression, and boldness with *C. citricola* spiders in the field from two diverging populations sharing the same core introduction. We highlighted significant trait correlations with Benjamini-Hochberg corrections in bold. Behaviors from the same assay are shaded similarly.

Range-level comparisons of all spiders in Florida (n=1223 spiders)				
Measured behavioral responses	Prey Attack Duration (s)	Latency to explore in a novel environment (s)	Total activity duration (s)	Latency to resume activity after predator stimulus (s)
Latency to Respond to Prey Stimulus (s)	**p < 0.0001** **ρ = -0.384**	p =0.4090 ρ = 0.0258	p = 0.0286 ρ = 0.0332	p = 0.0610 ρ = 0.0158
Prey Attack Duration (s)		**p < 0.0001** **ρ = 0.112**	p = 0.4300 ρ = -0.0246	p = 0.1280 ρ = 0.0472
Latency to explore in novel environment (s)			**p < 0.0001** **ρ = -0.238**	**p < 0.0001** **ρ = 0.132**
Total activity duration (s)				p = 0.0900 ρ = 0.0512
Core population (n=282)				
Measured behavioral responses	Prey Attack Duration (s)	Latency to explore in novel environment (s)	Total activity duration (s)	Latency to resume activity after predator stimulus (s)
Latency to Respond to Prey Stimulus (s)	**p< 0.0001** **ρ=-0.510**	p=0.540 ρ=-0.0408	p=0.480 ρ=0.0470	p=0.877 ρ= 0.0102
Prey Attack Duration (s)		p=0.0805 ρ=0.116	p= 0.575 ρ= -0.0373	p=0.0645 ρ=0.122
Latency to explore in novel environment (s)			**p=0.002** **ρ= -0.198**	**p< 0.0001** **ρ=0.392**
Total activity duration (s)				p=0.197 ρ=0.086

Table 5 continued

Eastern population (n=384)				
Measured behavioral responses	Prey Attack Duration (s)	Latency to explore in novel environment (s)	Total activity duration (s)	Latency to resume activity after predator stimulus (s)
Latency to Respond to Prey Stimulus (s)	**p< 0.0001 ρ=-0.316**	**p=0.0050 ρ=0.173**	p=0.345 ρ=-0.0594	p= 0.0705 ρ=0.113
Prey Attack Duration (s)		p=0.297 ρ=0.0660	p=0.0703 ρ=0.114	p= 0.255 ρ=0.0716
Latency to explore in novel environment (s)			p=0.451 ρ=-0.0478	**p=0.0010 ρ=0.206**
Total activity duration (s)				p=0.225 ρ=-0.0764
Western population (n=557)				
Measured behavioral responses	Prey Attack Duration (s)	Latency to explore in novel environment (s)	Total activity duration (s)	Latency to resume activity after predator stimulus (s)
Latency to Respond to Prey Stimulus (s)	**p< 0.0001 ρ=-0.375**	p=0.789 ρ=-0.0114	p=0.166 ρ=0.0589	p=0.640 ρ=-0.0199
Prey Attack Duration (s)		**p=0.009 ρ=0.111**	p=0.206 ρ=-0.0538	p= 0.999 ρ< 0.0001
Latency to explore in novel environment (s)			**p< 0.0001 ρ=-0.361**	p=0.0252 ρ=-0.0956
Total activity duration (s)				**p=0.169 ρ=0.0585**

Table 6. Logistic regression model outputs

Outputs for the full logistic regression models predicting the frequency of spiders responding to prey stimuli, attacking prey stimuli, exploring a novel arena, and resuming activity after a predator stimuli to population, length, and sex. Significant predictors are bolded.

Model for spiders responding to prey stimuli (n=1092)			
Predictors	*df*	χ^2	p-value
Intercept	1	54.1031	< 0.0001
Population	2	0.1908	0.9090
Sex	2	23.8120	< 0.0001
Length	1	6.0471	0.0139
Model for spiders attacking prey stimuli (n=1224)			
Predictors	*df*	χ^2	p-value
Intercept	1	29.7992	< 0.0001
Population	2	25.9219	< 0.0001
Sex	2	6.4389	0.0400
Length	1	1.0334	0.3094
Model for spiders exploring in a novel arena (n=1152)			
Predictors	*df*	χ^2	p-value
Intercept	1	38.2485	< 0.0001
Population	2	123.8255	< 0.0001
Sex	2	4.176	0.1214
Length	1	1.0567	0.3040
Model for spiders resuming activity after a predator stimulus (n=1166)			
Predictors	*df*	χ^2	p-value
Intercept	1	73.0936	< 0.0001
Population	2	49.3023	< 0.0001
Sex	2	0.8897	0.1214
Length	1	1.0939	0.3040

Table 7. Negative binomial outputs for spiders across Florida

Negative binomial model outputs predicting foraging aggression (latency to attack, attack duration), exploration/activity (latency to explore, total activity), and boldness (latency to resume activity after predator stimulus). Significant predictors are bolded.

Model for the latency of spiders to respond (n=520)			
Predictors	*df*	F	p-value
Population	2	12.9912	< 0.0001
Length	1	3.2221	0.0732
Sex	2	2.4349	0.0886
Model for the attack duration of spiders (n=520)			
Predictors	*df*	F	p-value
Population	2	3.3636	0.0354
Length	1	0.3582	0.5498
Sex	2	6.1244	0.0024
Model for the exploration latency of spiders (n=693)			
Predictors	*df*	F	p-value
Population	2	18.0285	< 0.0001
Length	1	0.3281	0.5670
Sex	2	0.7557	0.4701
Model for the total activity duration of spiders (n=693)			
Predictors	*df*	F	p-value
Population	2	3.9587	0.0195
Length	1	1.4353	0.2313
Sex	2	10.0108	< 0.0001
Model for the latency to resume activity after a predatory stimulus in spiders (n=856)			
Predictors	*df*	F	p-value
Population	2	16.5105	< 0.0001
Length	1	12.6401	0.0004
Sex	2	7.6897	0.0005

Table 8. Negative binomial model outputs for western spiders

Outputs for the full negative binomial regression models for western populations predicting foraging aggression (latency to attack, attack duration), exploration/activity (latency to explore, total activity), and boldness (latency to resume activity after predator stimulus) as function of latitude, sex, and length. Significant predictors are bolded.

Western Population			
Model for the latency of spiders to respond (n=265)			
Predictors	*df*	F	p-value
Latitude	1	1.0397	0.3088
Length	1	5.1342	0.0243
Sex	2	0.2826	0.7541
Model for the attack duration of spiders (n=265)			
Predictors	*df*	F	p-value
Latitude	1	5.6682	0.0180
Length	1	0.0010	0.9754
Sex	2	3.8099	0.0234
Model for the exploration latency of spiders (n=244)			
Predictors	*df*	F	p-value
Latitude	1	0.6913	0.4066
Length	1	2.3379	0.1276
Sex	2	2.5745	0.0783
Model for the total activity duration of spiders (n=244)			
Predictors	*df*	F	p-value
Latitude	1	2.1757	0.1415
Length	1	0.8188	0.3664
Sex	2	5.3258	0.0054
Model for the latency to resume activity after a predatory stimulus in spiders (n=354)			
Predictors	*df*	F	p-value
Latitude	1	0.7413	0.3898
Length	1	1.5396	0.2155
Sex	2	9.5592	< 0.0001

Table 9. Negative binomial model outputs for eastern spiders

Outputs for the full negative binomial regression models for eastern populations predicting foraging aggression (latency to attack, attack duration), exploration/activity (latency to explore, total activity), and boldness (latency to resume activity after predator stimulus) as function of latitude, sex, and length.

Eastern Population			
Model for the latency of spiders to respond (n=166)			
Predictors	*df*	F	p-value
Latitude	1	0.7921	0.3748
Length	1	6.8594	0.0097
Sex	2	1.1393	0.3226
Model for the attack duration of spiders (n=166)			
Predictors	*df*	F	p-value
Latitude	1	3.5198	0.0625
Length	1	0.2246	0.6362
Sex	2	3.0463	0.0502
Model for the exploration latency of spiders (n=270)			
Predictors	*df*	F	p-value
Latitude	1	1.4462	0.2302
Length	1	1.0685	0.3022
Sex	2	1.6197	0.1999
Model for the total activity duration of spiders (n=270)			
Predictors	*df*	F	p-value
Latitude	1	8.4262	0.0040
Length	1	0.9045	0.3424
Sex	2	4.3557	0.0138
Model for the latency to resume activity after a predatory stimulus in spiders (n=286)			
Predictors	*df*	F	p-value
Latitude	1	14.0162	0.0002
Length	1	8.4707	0.0039
Sex	2	0.0998	0.9051

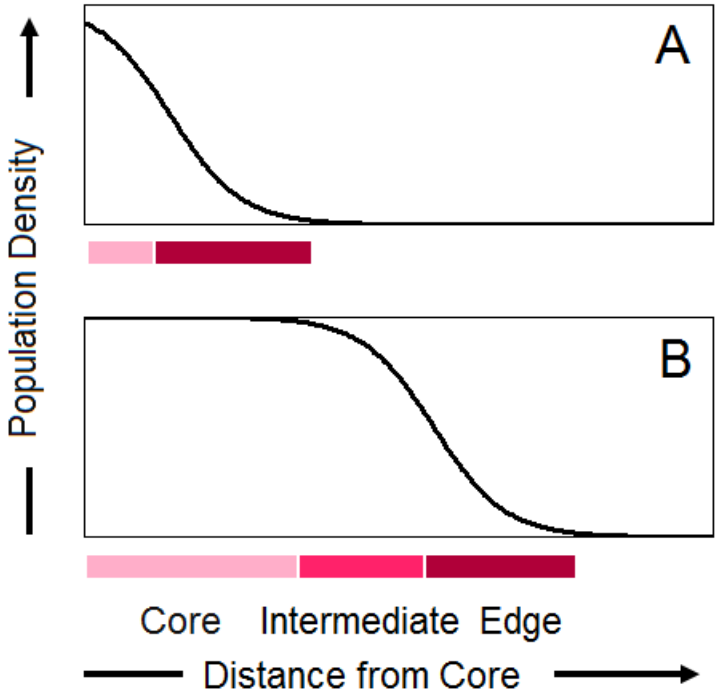

Figure 4. Population density in an expanding population over time

A population's expanding range over time, where population density falls with distance from the core. Over time, the range expands from an area with A) density growth across the range to B) the core eventually reach carrying capacity, promoting more dispersal towards the edge and areas with intermediate colonization history.

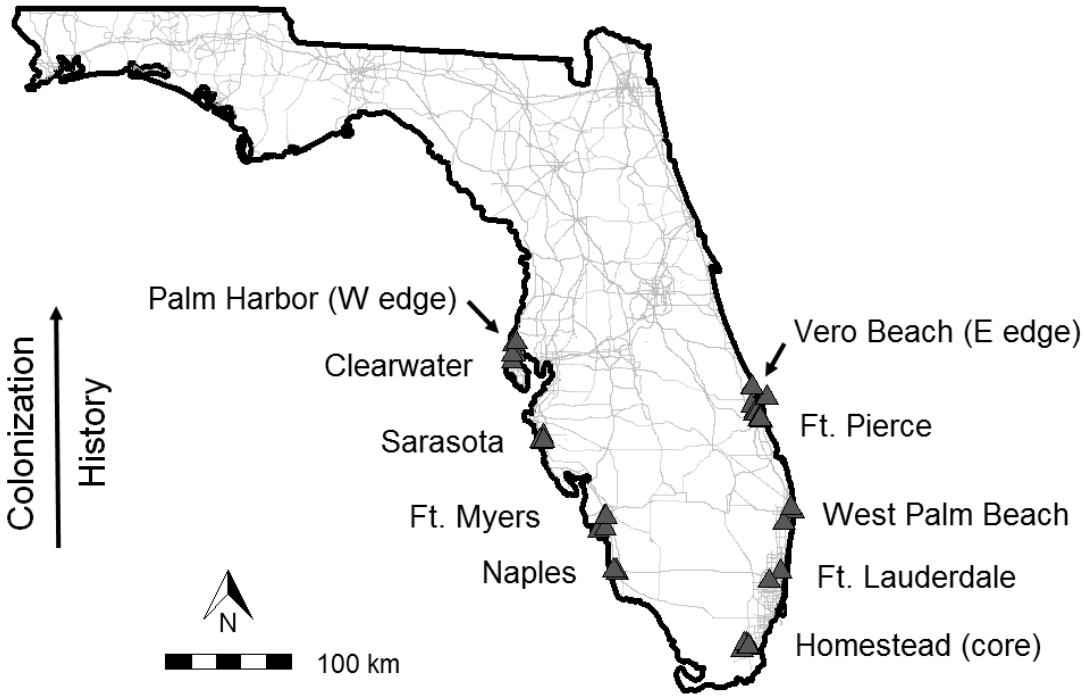

Figure 5. Map of *C. citricola*'s range expansion in Florida

The extent of *C. citricola*'s non-native range in Florida as of August 2017, sites chosen for behavioral assays and spider collection are denoted by shaded triangles. Homestead is the core established site, and Palm Harbor and Vero Beach are at the leading edge of each coastal population. Grey areas are major roads in the state, as a proxy for human settlement and urbanization.

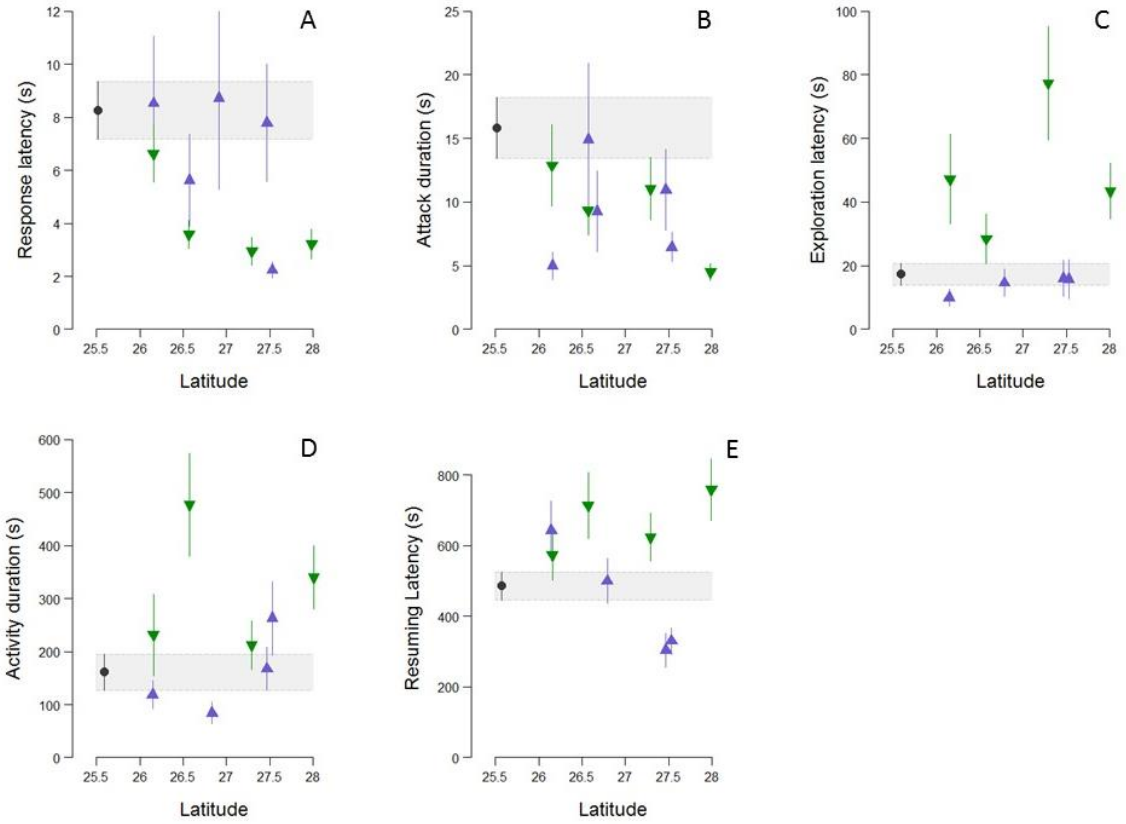

Figure 6. Mean behavioral scores of cities over latitude

The mean behavioral scores and 95% confidence intervals over latitude, where each point show the average score of each city. Latitude is a proxy for distance from the core (Homestead) and colonization history. Green triangles indicate western population cities, whereas purple triangles indicate eastern population cities. The shaded area delineates the 95% confidence interval for the core population, to offer comparison across the range.

CHAPTER III
DOES SPATIAL SORTING EXPLAIN LEADING EDGE PERSONALITY TYPES IN A SPIDER'S NON-NATIVE RANGE?

Abstract

Expanding populations are often characterized by phenotypic shifts across the range. The composition of phenotypes found at leading edges may differ from those found at the population core, because spatial sorting can result in the most dispersive individuals at range fronts. *Cyrtophora citricola* is an orbweaver spider with two expanding populations originating from the same core in its non-native Florida range. Since spiders at the leading edges were previously found to differ in various personality traits from those at the core, we tested laboratory-raised spiderlings for dispersal tendency to determine whether spatial sorting can account for these patterns. Spiders from the leading edge of the eastern population were more dispersive than those at the core, and the western spiders were the least dispersive of the three populations. Dispersal propensity was correlated with the activity and exploratory tendencies of individuals. Population-level differences we had previously observed for foraging aggression and activity were not found in the captive-raised spiders, suggesting that they represent plastic responses to environmental conditions. However, mean population-level differences in exploration and boldness were maintained in captivity, suggesting that these behaviors have a heritable component. Overall, the eastern spiders were characterized by being bolder, whereas the western spiders were the least bold and exploratory. While this study provides evidence of spatial sorting of more dispersive, exploratory, and active individuals in the eastern population, the divergence in risk-taking behaviors between the two populations highlight the importance of understanding the interactions between natural and spatial selection.

Introduction

Ecosystems are regularly in flux, and more so recently with accelerating anthropogenic processes, including habitat fragmentation, urbanization, climate change, and unintentional species introductions (Seto et al. 2012, Newbold et al. 2015, Urban 2015, Sardain et al. 2019). Species may respond to these changes through range contractions or expansions (Travis and Dytham 2002, Jetz et al. 2007, Sexton et al. 2009, Nadeau and Urban 2019). Non-native species introduced to favorable environments in particular often extend their range beyond the area of initial establishment.

Range expansions are dynamic, characterized by dispersal (Travis and Dytham 2002). Dispersal is defined as an individual's movement away from a natal site or social group (Ronce 2007, Clobert et al. 2009, Travis et al. 2012). In expanding ranges, the occupation of suitable habitats in the core and

intermediate of a range results in the net dispersal of individuals towards the leading edge. Dispersal tendency and ability varies among individuals in a population, much like other traits that determine the success and rate of colonization.

Spatial sorting is a process associated with range expansions that describes the accumulation of dispersive phenotypes found at expanding range fronts (Shine et al. 2011). Like runners in a foot race, more dispersive individuals are expected to be found further from an area of origin compared to their less dispersive counterparts. This can reflect the contributions of a host of traits impacting dispersal, such as longer limb length, higher movement rate (Phillips et al. 2006, Courant et al. 2019), greater stamina (Llewelyn et al. 2010), higher wing aspect ratio (Hassall et al. 2009), increased flight muscle ratio (Therry et al. 2014), and a greater tendency to explore novel habitats (Liebl and Martin 2012).

Spatial sorting can represent the shuffling of either plastic or heritable dispersive phenotypes across an expansion gradient. If range expansion continues over many generations, trait evolution can occur among heritable traits promoting dispersal. This is because lower population density and higher proportions of dispersive phenotypes at the leading edge create a higher chance of dispersive individuals mating, in a phenomenon known as the “Olympic Village effect” (Phillips et al. 2010). If dispersal is heritable, leading edge offspring produced by these pairings may be equally or more dispersive than their parents. Dispersal-correlated traits may show similar patterns of selection at range margins. Spatial selection can be considered as an alternative hypothesis to natural selection for explaining how traits evolve at range fronts, because low density and dispersal drive phenotypic patterns rather than adaptation to local conditions.

Understanding the mechanisms underlying phenotypic trait shifts along expanding gradients may allow us to predict the longevity of these patterns. Spatial sorting predicts that as the expansion wave moves through a location, the frequency of highly dispersive individuals diminishes over time, as admixture occurs between high and average dispersers when slower expansion waves colonize former edge sites (Travis and Dytham 2002). Since range expansion cannot continue forever, the effects of spatial sorting are expected to recede once a barrier to expansion is met. At the edge, rare alleles can temporarily surf to higher than average frequencies as a result of genetic drift and founder effects, regardless of their adaptive value (Travis et al. 2007). As barriers to expansion stabilize range boundaries, phenotypes may become more locally adapted to environmental conditions, leading to more stable range-wide patterns.

Cyrtophora citricola (Forskål 1775) is an orbweaver spider that has rapidly expanded its range in Florida since its discovery in 2000 (Edwards 2006). Two

branching populations have spread northward over 250 km along the western and eastern coast of Florida from the same origin of Homestead, near the southern tip of the state. We previously reported that leading edge spiders respond and attack prey stimuli faster and exhibit longer periods of activity in novel environments. However, *C. citricola* from the western population have seemingly diverged from those in the eastern population in boldness—range front spiders from the western population are less bold, whereas eastern spiders are bolder. Western spiders were also less exploratory, compared to eastern spiders that showed similar exploration latencies as those in the core.

In this study, we tested the hypothesis that spatial sorting underlies both expanding populations, and that phenotypic patterns previously observed from wild spiders across the expanding ranges of these two replicate populations are owing to personality-related dispersal. We predicted that clinal patterns found in both populations (i.e. faster response to prey, faster prey attacks, and activity duration in novel environments) are from correlations between these behaviors and dispersal tendency. Behavioral divergences in exploratory behavior and boldness were hypothesized to be responses from differing selective pressures in each population, where greater dispersal tendency was not correlated to these traits. We used a common garden approach to further determine whether behaviors represent plastic or genetic responses. This information is needed to better understand the longevity of phenotypic patterns across the range.

Methods

Study organism and introduction history

We focused this study on the colonial tentweb orbweaver spider, *Cyrtophora citricola*. While originally described from areas of the Old World including the Mediterranean, Middle East, Asia, and Africa (Forskål 1775, Kullmann 1958, 1959), *C. citricola* has established multiple new populations in the Americas and Caribbean in the last twenty years (Florez Daza 1996, Alayon Garcia et al. 2001, Alayon Garcia 2003, Garcia 2003, Alvares and De Maria 2004, Starr 2005, Viquez 2007). In 2002, the *C. citricola* population in Florida was surveyed for the first time. Its range was reported to be restricted within the city limits of Homestead, near the southern tip of the state (Edwards 2006).

Our subsequent surveys from 2014-2017 showed that *C. citricola* has expanded its range from the initial Homestead core. Despite tolerating a variety of plant substrates (Edwards 2006), *C. citricola* seems to prefer sturdy substrates for its extensive webs and open habitats exposed to full sunlight (Madrigal Brenes 2012, Chuang and Leppanen 2018). As such, it is absent in many of Florida's natural habitats, such as pinelands, grasslands, and swamplands at the center of the state. Instead, it is found in high densities in urban habitats along the western and eastern coasts. For this study, we collected them from urban

manmade substrates, such as guard rails, street signs, bridge railings, and building structures.

We consider the northward spread along the western and eastern coasts of Florida to represent two independent range expansions from populations sharing a common origin, Homestead. At the time of our last survey in August 2017, the northern range edges were at latitude 27.7156856 (Vero Beach, FL) of the east coast and latitude 28.12911484 (Palm Harbor, FL) on the west coast.

Field collection

We assayed spiders in the field from four different cities along their eastern and western expansion gradients, and the results of these assays are reported in Chapter 2. These locations extend northward along a latitudinal gradient that represents newer colonization times: Eastern population – Ft. Lauderdale (26.1412497), West Palm Beach (26.7420741), Ft. Pierce (27.4294654), and Vero Beach (27.645231). Western population – Naples (26.1449798), Ft. Myers (26.6187703), Sarasota (27.335939), and Clearwater/Palm Harbor (28.12911484). The eastern population was assayed in July 2015, and the western population was assayed in July 2017.

We also collected egg sacs from each location to raise spiders in a common garden environment. This study allowed us understand whether the behaviors we observed from the field mostly represent plastic or genetic responses to environments. Each egg sac was individually collected and maintained in a 2 oz. clear polypropylene containers with clear polyethylene lids. We transferred the egg sacs to The University of Tennessee (Knoxville, Tennessee, USA), where they were maintained in laboratory conditions.

Laboratory and common garden set up

In the laboratory, we kept egg sacs and spiderlings at 21.0-23.5°C with a 14:10 light: dark hour photoperiod. We misted the individually-contained egg sacs weekly with water until spiderlings emerged. Within a week of emergence, we moved groups of five spiderlings into new 2 oz. polypropylene containers. This was to ensure higher survival rates since we previously observed that solitary spiderlings often built insufficient webs, fed infrequently on *Drosophila* flies, and suffered a high (>90%) mortality rate (Chuang, personal observation). In groups, the first and second post-emergence instars seemed to tolerate sharing prey or scavenge from remains, leading to lower overall mortality rates (~40 - 60%).

In the lab, we fed the spiders *ad libitum* and misted them on a weekly basis. We fed them a mix of size-matched *Drosophila melanogaster* fruit flies, *Reticulitermes* sp. termites, and *Acheta domesticus* crickets. After the first behavioral trial (dispersal assay), we moved each third-instar individual into its own plastic 16 oz. deli container. This was performed to avoid cannibalism events and to maintain individual identity, since colored powders and paints

could not be safely applied and result in reliable distinction at that stage (Chuang, personal observation). Each spider container was labeled with an identity number indexed with field data including GPS coordinates of where its egg sac was collected. This information was not included on labels to reduce experimenter bias to treatment groups (e.g. site names, “core” vs. “edge”).

Behavioral assays

We used behavioral assays adapted from standard assays developed to measure spider behavior (Riechert and Hedrick 1993, Pruitt et al. 2008, Kralj-Fiser and Schneider 2012, Grinsted et al. 2013, Pruitt and Keiser 2014) and all but the dispersal assay are described in Chapter 2. We measured the dispersal tendency of all individuals at least once, although 66 were selected for three total measurements in order to determine how repeatable dispersal behaviors were. We waited two to three weeks following the dispersal assay (and introduction to a solitary, larger container) to conduct assays on foraging aggression, exploration/activity, and boldness. Each assay was conducted three times over the course of the next four weeks, since repeatability estimates are not known to significantly change with more observations (Bell et al. 2009). We cleaned the assay equipment with ethanol between assays to eliminate any deposited silk as well as chemical or olfactory cues.

Dispersal tendency

Spider dispersal involves a form of aerial movement known as “ballooning”, which involves the individual releasing dragline that is picked up by air currents (Bristowe, 1939). Spiders usually balloon as early juveniles (Richter 1970, Greenstone et al. 1987), and experiments with native *C. citricola* suggest that all juvenile instars will balloon (Johannesen et al. 2012). Given this, we chose to test spiders within the second to fourth post-emergence instars. Since spider ballooning is influenced by external factors such as time of day, temperature changes, wind speed, light, and meteorological conditions (Weyman 1993) and individual aeronauts can be difficult to recover afterwards, it is difficult to test dispersal behaviors in wild populations. As such, we tested spider dispersal from those raised in a laboratory common garden environment.

“Tiptoeing” and “rappelling” behaviors precede ballooning aerial dispersal (Weyman 1993, Bonte et al. 2003, Entling et al. 2011, Ventura et al. 2017). An individual initiates ballooning by climbing to the top of a structure, straightening its legs in a “tiptoe” posture, tilting its abdomen up, and releasing a silken dragline from the spinnerets. The air current picks up the dragline, rendering the spider airborne. An individual rappels when it drops from the structure and floats on air currents while remaining anchored to the wooden stand. It then initiates ballooning by biting the silken strands and releasing itself into air currents. We

did not distinguish between tiptoeing and rappelling behaviors in the laboratory, and used both as a proxy for dispersal tendency.

Our dispersal trial protocol for *C. citricola* was modeled after Ventura et al., who used an arena consisting of a vertical wooden dowel (30 cm, 1cm diameter) fixed on a plastic stand (2017) (Figure 1). The stand was immersed in a 150mm x 65mm petri dish with water to prevent spiders from walking off the dowel. A fan was placed 1m away at a 65° angle, and used to simulate air moving at < 3m/s to create conditions conducive to ballooning (Greenstone 1990, Sheldon et al. 2017). Spiderlings were fed 4-7 *Drosophila* flies the day before the assays and testing occurred between 0800 and 1200 hours.

We released each spiderling at the top of the wooden dowel for each five minute trial. Individuals generally explored the dowel by walking up and down its length a few times before initiating dispersal behaviors. Five minutes was determined to be long enough to observe several tiptoeing events (Ventura et al. 2017).

Foraging aggression

We measured the latency of individuals to attack a prey stimulus by applying an electronic gum stimulator (BrushPoint Vital Health Power Oral-B Care System) to the edge of each web in a 16 oz. container. The gyrating sensations from the rubber tip stimulate struggling prey on a web and elicit foraging behaviors from *C. citricola*. We measured the latency for the individuals to respond to the vibrations, the latency to mount a full attack on the gum stimulator, and calculated the total duration of the attack based on the difference in these two times. An attack was only considered successful if the spider bit the rubber tip; we cut the trial off after 120 seconds otherwise.

Exploration/activity

We placed each individual into an empty 150 mm x 65 mm Petri dish and allowed it to freely explore this novel space. *C. citricola* usually responded to the relocation with a "huddle" response that is typical to spiders, which involves freezing and folding its legs into its body, akin to thanatosis. We measured the latency for an individual to begin exploration following introduction. Exploratory activity was defined as any movement that displaced the individual, as this involved laying down silk every few seconds. Exploration included walking along the bottom surface, scaling the walls of the arena, as well as initiating web-building activities. We also measured the total amount of time spent in activity. This assay ended once the spider had ceased activity for five consecutive minutes.

Boldness

We defined boldness as an individual's propensity to engage in risky behaviors in a novel environment. We began the boldness trial following the exploration/activity assay; after each individual stopped exploring for five minutes, we puffed them twice with a rubber bulb from 3 cm away. The quick puffs of air simulate an aerial predator approach (Riechert and Hedrick 1993, Pruitt et al. 2011), which results in all individuals huddling. We then measured how long it took for each to resume normal activity, such as walking and web-building activities. Each spider was given up to 60 minutes to resume activity.

Statistical Methods

Since animal personality is defined as the consistency of individual differences in behavior across time and contexts (Sih et al. 2004), behavioral repeatability is quantified to demonstrate consistency over time. It determines the proportion of variation that is explained by differences between individuals (Bell et al. 2009). To determine whether dispersal behaviors were repeatable, we used the R package rptR to calculate the repeatabilities of tiptoe latency and tiptoe frequency in 67 juveniles that had been assayed three times over 14 days (Stoffel et al. 2017). Since the 95% confidence interval for tiptoe frequency repeatability overlapped with 0, we did not consider that to be a repeatable trait, and used tiptoe latency for behavioral comparisons going forward.

We used logistic regressions to model the effect of population (eastern, western, core) and latitude on the proportion of spiderlings engaging in tiptoe behavior, which was a binomially distributed response. We incorporated potential confounding variables, sex and length, as direct effects in the models. Sex was a categorical variable, including male, female, and unknown juveniles as a category. Although all individuals were juveniles, they were classified as "unknown" if they were less than 3mm in length, and could not be sexed based on external genital morphology yet.

We used negative binomial regression models to model the effect of these same factors on tiptoe latency, and created individual models for the western and eastern populations to determine whether latitude predicted tiptoe latency. Models were initially fit with all the factors and interactions as direct effects, and we used AIC criterion to select the best models. To determine whether foraging aggression, exploration/activity, and boldness are correlated to dispersal, we conducted pairwise Spearman's correlations between these behaviors and tiptoe latency. We used Benjamini-Hochberg corrections on our p-values to reduce changes of Type I errors (Benjamini and Hochberg 1995). Lastly, we tested the effects of population, source, their interaction, as well as potential confounding factors such as latitude, length, and sex on a dataset comprised of behavioral responses from our common garden as well as field data (results previously reported in Chapter 2). This allowed us to determine how responses varied from

wild individuals assayed *in situ* compared to those raised in captivity, to better allow us to understand how environmental plasticity might underlie the observed behaviors. We analyzed all data in R (R Core Team 2019).

Results

Repeatability of dispersal

Of the two dispersal-related behaviors measured, tiptoe count and latency, only tiptoe latency was found to be repeatable ($r = 0.290$, $n = 65$, 95 CI = (0.095, 0.404)) (Table 1). Since the 95% confidence interval of the correlation coefficient for tiptoe frequency overlapped with 0, we rejected its repeatability ($r = 0.113$, $n = 67$, 95% CI = (0, 0.211)). As such, we only consider dispersal latency to be a personality trait. We previously showed that foraging aggression, exploration/activity, and boldness were repeatable in Chapter 2.

Differences in dispersal between populations

We found that population alone had a significant effect on the likelihood of spiders tiptoeing ($\chi^2 = 16.942$, $df = 2$, $p = 0.0002$). Our Tukey HSD test showed that while neither eastern or western populations differed significantly from the core, western spiders were less likely to tiptoe than eastern spiders ($\bar{x} = -0.1658$, 95% CI = (-0.2564, -0.0751), $p < 0.0001$). Similarly, while the core and eastern populations did not differ significantly in how quickly spiders tiptoed, eastern spiders were faster to tiptoe compared to western spiders ($\bar{x} = -0.2483$, 95% CI = (-0.4023, -0.0943), $p = 0.0005$) (Table 2). In the western population, latitude was not found to be a significant predictor of dispersal behaviors; in fact, the best model selected for this population was the null model (Intercept = 4.8712, $Z=103.6$, $p < 0.0001$). However, spiders from the eastern population had faster latencies to tiptoe at higher latitudes ($F = 28.912$, $df = 1$, $p < 0.0001$) (Table 3), corresponding to newer colonization sites (Figure 2).

Dispersal syndromes

We tested whether dispersal latency in lab-raised *C. citricola* spiderlings were correlated to other behavioral traits. We further separated our analyses by range, to determine whether different dispersal syndromes were detected between the core, eastern, and western parts of the range. In general, boldness and foraging aggression were not correlated to our measure of dispersal tendency (Table 5). However, some measures of exploration and activity were correlated with dispersal. For all three range portions, spiders that tiptoed faster also tended to be more active (Core: $\rho = -0.441$, $n = 58$, $p = 0.0005$; East: $\rho = -0.439$, $n = 68$, $p = 0.0001$; West: $\rho = -0.305$, $n = 67$, $p < 0.0001$), begin exploring faster (Core: $\rho = 0.472$, $n = 58$, $p = 0.0001$; East: $\rho = 0.451$, $n = 68$, $p = 0.0001$; West: $\rho = 0.296$, $n = 67$, $p < 0.0001$), and tiptoe more frequently (Core: $\rho =$ -

0.637, n = 58, $p < 0.0001$; East: $\rho = -0.588$, n = 68, $p < 0.0001$; West: $\rho = -0.729$, n = 67, $p < 0.0001$) (Figure 3).

Common garden vs. wild individual behaviors

We found that common garden spiders differed from their field counterparts in aggressive behaviors and time spent in activity (Table 6; Figure 4). Spiders raised in laboratory conditions were faster to respond and attack prey stimuli ($F_{1,1410} = 33.9315$, $p < 0.0001$; $F_{1,1753} = 118.7261$, $p < 0.0001$) and spent more time moving in a novel environment ($F_{1,923} = 4.8210$, $p = 0.0284$) than their field counterparts. Similarly, common garden spiders were more likely to respond and attack than spiders assayed from the field ($\chi^2 = 21.5571$, $p < 0.0001$; $\chi^2 = 157.31$, $p < 0.0001$). In contrast, behaviors relating to risk-taking in novel environments, namely exploration and boldness, were not different between field and common garden spiders; instead, similar population-level differences described in Chapter 2 emerged. Western spiders were least likely to explore ($\chi^2 = 124.0700$, $p < 0.0001$), whereas the eastern spiders were more likely to explore and resume activity after a predatory stimulus ($\chi^2 = 42.9317$, $p < 0.0001$). We also found that eastern spiders were the fastest to initiate exploration and resume activity ($F_{2,1680} = 52.3191$, $p < 0.0001$; $F_{2,1489} = 34.8198$, $p < 0.0001$).

Discussion

Our study tested the spatial sorting hypothesis on two replicate expanding populations of *C. citricola* to determine whether the previously reported behavioral clines (e.g. higher aggression, greater activity, boldness) are linked to dispersal and range expansion. Spiders from the eastern population were, indeed, progressively more dispersive across their expansion gradient. This pattern likely drives our finding that eastern spiders were more dispersive compared to western spiders. Faster dispersers, in turn, were generally more active and more exploratory, which may account for patterns of more active individuals at this spider's leading edge. Therefore, we found partial support for spatial sorting as a mechanism underlying phenotypic shifts. Although we detected a positive exploration-dispersal relationship between all populations, it was notably weaker in the western population. Western spiders showed more variable, but overall lower levels of exploration and dispersal.

Although spatial sorting likely underlies some of the phenotypic patterns observed in *C. citricola*'s non-native range expansions, it does not explain the divergence of boldness between populations that we reported in Chapter 2. Boldness and exploratory tendencies are correlated in each population. It likely represents an individual's willingness to expose itself to risk and novelty, with eastern and western populations characterized by increasingly risk-prone and risk-averse individuals towards the edge, respectively. While boldness itself does

not seem to be a trait that is being spatially sorted through dispersal, it may instead be shaped by natural selection from differing environmental conditions at both populations as well as conditions characteristic at range fronts (e.g. naïve predators, lower pathogen and parasite density, lower competition from conspecifics, more available habitats, etc.) (Sexton et al. 2009).

Personality types undergoing dispersal-driven spatial sorting are not immune to the effects of natural selection. Thus, the patterns we observed likely represent the results of both processes on phenotypic composition (Van Petegem et al. 2016). The interaction of both processes leads to interesting directions for future study—namely, the strength of spatial selection compared to natural selection, especially in cases leading to opposing selective forces. We propose that the strength of spatial selection on phenotypic composition will likely increase under idealized spatial sorting conditions. These include conditions leading to 1) relatively isolated leading individuals 2) at low densities. Rapid expansions from invasive species spreading over large swaths of habitable space can lead to such patterns. Unsurprisingly, some of the best known cases of spatial sorting involve invasive species (Bohn et al. 2004, Phillips et al. 2006, Hudina et al. 2012, Liebl and Martin 2012, Lopez et al. 2012, Laparie et al. 2013). If dispersal is 3) heritable and 4) has a direct effect on the distance travelled, subsequent generations may be capable of maintaining low densities of dispersive leading edge individuals. These conditions are thought to promote patterns similar to runaway selection (Phillips et al. 2010), where alleles can "surf" at the leading edge regardless of adaptive value (Klopfstein et al. 2006, Travis et al. 2007, Excoffier and Ray 2008).

Since we measured dispersal tendency in *C. citricola*, which likely only has an indirect effect on overall displacement, it is notable that we were able to detect signatures of dispersal-driven spatial sorting. Like other spider species, *C. citricola* engages in passive dispersal instead of active dispersal. While individuals ultimately decide on whether to tiptoe and balloon (Bonte and Lens 2007), it is unclear how much they can influence the length of their travel, beyond adjusting body posture to influence terminal velocities (Suter 1992). The general paradigm is that ballooning spiderlings are part of the "aerial plankton" and that their trajectory and destination are ultimately at the mercy of air currents and abiotic factors (Glick 1939, Thomas et al. 2003, Bell et al. 2005). Dispersing under turbulent conditions such as high wind speeds can pose high risks, which may be why spiders generally disperse under specific meteorological conditions and wind speeds (< 3 m/s) (Weyman et al. 2002). Even at low wind speeds (1.5-2.9 m/s), theoretical models suggest that more than 40% of individuals can be displaced over half a kilometer. Given the current understanding that spiderlings have limited control over the distance they balloon, it is possible that individuals

that choose to disperse already represent a distinct subsample of the population. A more dispersive individual may also engage in more ballooning events, as our assays showed.

Ballooning dispersal does not appear to be an obligatory life history event for *C. citricola*. Johannesen et al. report that only 35-50% of native *C. citricola* population disperse in semi-wild conditions in Israel (2002), which is a much lower percentage than the 74 - 90% we found when testing them under ideal ballooning conditions in the laboratory. Ballooning motivation in arachnids has been shown to exhibit some heritability (Bonte and Lens 2007), and we further found that faster dispersers tended to try ballooning more frequently. This lends further support that ballooning behavior can undergo both spatial sorting and selection at the leading edges of *C. citricola*'s populations.

The signature of spatial sorting is further expected to be clearest while range expansion is current and has been ongoing long enough for distinct phenotypic patterns to emerge. *Cyrtophora citricola* had already expanded over 350 and 280 km in the western and eastern populations prior to this study. From 2014 to 2017, we documented range expansions of about 22 and 32 kilometers in the western and eastern populations respectively. While the range expansion was current during this study, it is unclear how much further north these populations will expand. *C. citricola* purportedly does not survive in freezing temperatures (Edwards 2006), so barring physiological adaptation to cooler climate, these two populations may reach a thermal barrier to further establishment.

Our findings that aggression and activeness represent more plastic traits whereas exploration and boldness represent heritable traits with stronger genetic underpinnings have implications for the longevity of phenotypic composition at each site. As the expansion front passes leading edge sites, subsequent waves of individuals will colonize and net dispersal from the core will lead to occupation of average dispersers to intermediate sites. As the effect of dispersal-driven spatial sorting wanes at each site, phenotypes may become increasingly locally adapted to local environmental pressures. If conditions at former edge sites select for individuals differing from initial leading edge phenotypes, we expect phenotypic turnover in subsequent cohorts or generations to occur faster in plastic traits we observed than heritable traits.

Cyrtophora citricola's status as a non-native species to North America has implications for the phenotypic shifts towards more aggressive, active, and either shy or bold individuals at the leading edge that we have reported. Aggressive spiders are known to engage in superfluous killing behaviors, often attacking more prey than they consume (Maupin and Riechert 2001). The aggression and boldness of individuals has been known to impact the likelihood of colony-level

survival in social spiders (Pruitt and Keiser 2014), in part by mitigating negative impacts of web-sharing heterospecific spiders that are common in colonies (Pruitt et al. 2012, Keiser and Pruitt 2014). While *C. citricola*'s role in its new introduced community remains unclear, it is known that different personality types can have different community-level interactions (Sih et al. 2012). Ergo the ephemerality of phenotypic patterns that can result from the spatial sorting process can likewise have community-wide effects that warrant future study.

In this study, we measured the dispersal tendencies of common garden *C. citricola* spiders and showed that leading edge spiders in the eastern population tend to be more dispersive. Activity and exploration may represent spatially sorted traits, whereas other behavioral patterns are likely responses to environmental conditions present in each population. We found that population-level differences in risk-taking behaviors remained even in common garden spiderlings, while aggression and activity did not. This plasticity in activity suggests that leading edge sites may see the fastest turnover in this personality type in the future, if activity is not adaptive. Further work will ideally better understand the interaction between spatial sorting and adaptive processes shaping personality traits across both populations.

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Appendix C

Table 10. Repeatability estimates of dispersal behaviors

Spiders raised in a common garden environment showed repeatability in tiptoe latency, but not tiptoe frequency.

Dispersal Assay	R	SE	95% CI	p
Latency to tiptoe	0.290	0.079	(0.095, 0.404)	<0.0001
Frequency of tiptoes	0.113	0.063	(0, 0.211)	0.0581

Table 11. Population and length predict tiptoe latency in *C. citricola* in all assayed populations

Model for the latency of spiders to tiptoe (n=454)			
Predictors	*df*	F	p-value
Population	2	4.4397	0.0124
Length	1	25.5934	< 0.0001

Table 12. Tiptoe latency by latitude in the eastern population

Latitude and sex best predicted the latency for spiders from the eastern population to tiptoe.

Model for the latency of spiders to tiptoe (n=156)			
df	*df*	*df*	*df*
1	1	1	1
2	2	2	2

Table 13. Spearman's pairwise comparisons with dispersal tendency

Spearman's ρ pairwise comparisons between behavioral variables measuring exploration/activity, foraging aggression, and boldness and measures of dispersal for *C. citricola* spiders raised in a common garden conditions. Bolded variables represent statistically significant values after using the Benjamini-Hochberg correction.

Behaviors	Measured responses	Latency to tiptoe (s)		
		Core (n=57)	Eastern Population (n=69)	Western Population (n=60)
Foraging Aggression	Latency to respond to prey stimulus (s)	p = 0.2183 ρ = 0.1656	p = 0.55997 ρ = -0.0714	p = 0.0626 ρ = -0.0643
	Prey attack duration (s)	p = 0.6134 ρ = -0.0683	p = 0.5210 ρ = 0.0786	p = 0.0876 ρ = -0.0205
Exploration/ Activity	Latency to explore in novel environment (s)	**p < 0.0001** **ρ = 0.4969**	**p < 0.0001** **ρ = 0.6520**	**p = 0.0034** **ρ = 0.3719**
	Total duration of activity (s)	p = 0.76935 ρ = -0.0533	**p = 0.0071** **ρ = -0.3213**	**p = 0.0157** **ρ = -0.3107**
Boldness	Latency to resume activity after predator stimulus (s)	p = 0.6464 ρ = 0.0621	p = 0.1581 ρ = -0.1718	p = 0.3280 ρ = 0.1284
Dispersal	Tiptoe count	**p < 0.0001** **ρ = -0.7136**	**p = 0.0010** **ρ =-0.2962**	**p < 0.0001** **ρ = -0.679**

Table 14. Common garden vs. field spider behaviors

We tested the effects of population (eastern, western, and core), source (wild or common garden), their interaction, as well as latitude, length, and sex of individuals on the behavioral traits of interest. The main effects included below are based on the best models selected from AIC criterion. Values that are statistically significant ($p < 0.05$) are bolded.

	Factors from best model					
Behavioral responses	Population	Source	Latitude	Length	Sex	Population *Source
Latency to Respond (s)		**$F_{1,1410}$ = 33.9315 p < 0.0001**	$F_{1,1410}$ = 3.6578 p = 0.0560	**$F_{1,1410}$ = 5.2174 p = 0.0225**	**$F_{2,1409}$ = 20.7085 p < 0.0001**	
Attack Duration (s)	**$F_{2, 1752}$ = 9.2160 p = 0.0001**	**$F_{1, 1753}$ = 118.7261 p < 0.0001**		**$F_{1, 1753}$ = 7.2305 p = 0.0007**	$F_{1, 1753}$ = 2.7764 p = 0.0626	**$F_{2, 1752}$ = 19.9620 p < 0.0001**
Latency to Explore (s)	**$F_{2,1680}$ = 52.3191 p < 0.0001**	$F_{1,1681}$ = 0.3222 p = 0.7115	**$F_{1,1681}$ =5.9553 p = 0.0148**	$F_{1,1681}$ = 0.0218 p = 0.8827	$F_{2,1680}$ = 4864 p = 0.6149	$F_{2,1680}$ = 1.7369 p = 0.1764
Total Activity (s)	**$F_{2,922}$ = 3.5726 p = 0.0285**	**$F_{1,923}$ = 4.419 p = 0.0297**	**$F_{1,923}$ = 4.8210 p =0.0284**	$F_{1,923}$ = 2.3283 p = 0.1274	**$F_{2,922}$ = 13.5694 p < 0.0001**	
Latency to Resume (s)	**$F_{2,1489}$ = 34.8198 p < 0.0001**	$F_{1,1490}$ = 0.9662 p = 0.6631		**$F_{1,1490}$ = 7.1014 p = 0.0078**		**$F_{2,1489}$ = 4.3683 p = 0.0128**
Prey response proportion		**χ^2 = 21.5571 p < 0.0001**		**χ^2 = 5.8285 p = 0.0158**	**χ^2 = 28.6865 p < 0.0001**	
Attack completion proportion	**χ^2 = 18.3314 p = 0.0001**	**χ^2 = 157.31 p < 0.0001**	**χ^2 = 75.9310 p < 0.0001**	**χ^2 = 3.0652 p = 0.0800**	**χ^2 = 12.8168 p = 0.0016**	**χ^2 = 48.4511 p < 0.0001**
Exploration initiation proportion	**χ^2 = 124.07 p < 0.0001**	χ^2 = 0.7266 p = 0.3940				
Resuming activity proportion	**χ^2 = 42.9317 p < 0.0001**	χ^2 = 0.0025 p = 0.9598	**χ^2 = 5.0249 p = 0.0250**	χ^2 = 0.9798 p = 0.3222	χ^2 = 0.6661 p = 0.7167	

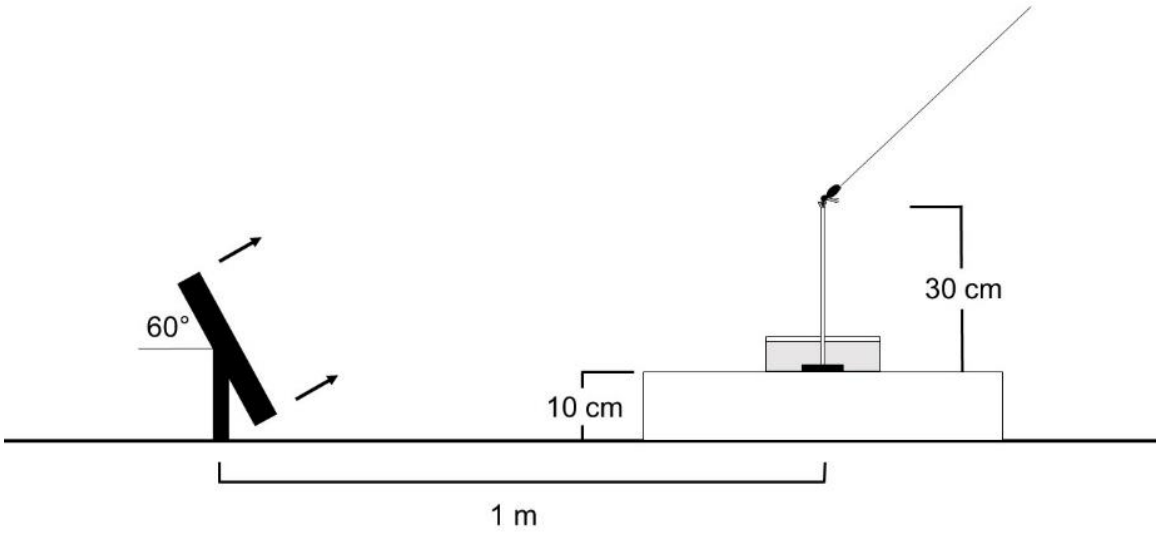

Figure 7. The dispersal assay set up

We placed a wooden dowel within a water-filled arena with a 60° tilted fan placed 1m from the testing arena. We then released a spiderling on the dowel tip to explore. We measured its latency to initiate ballooning behaviors and capped the trial at 5 minutes.

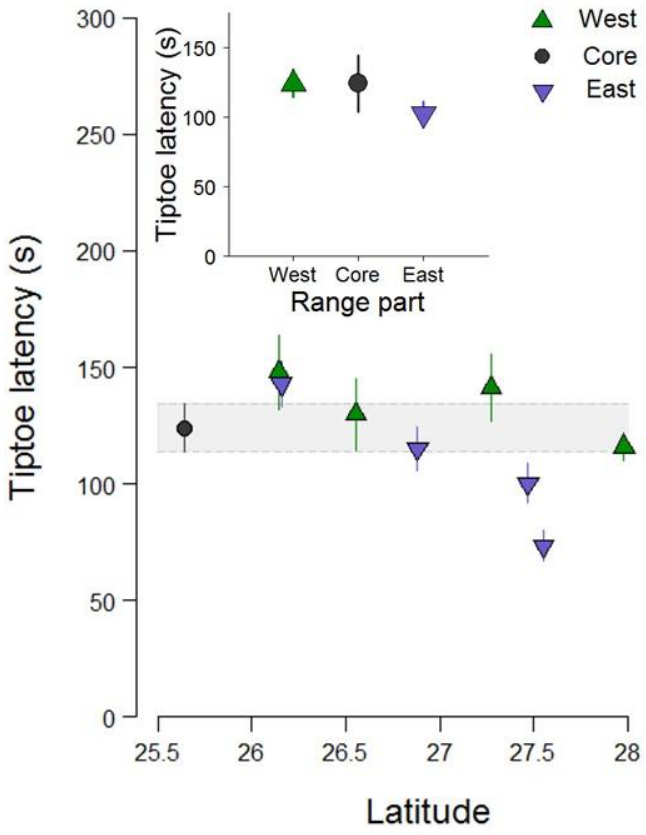

Figure 8. Mean dispersal personalities across the expansion gradient

We plotted mean tiptoe latencies and 95% confidence intervals across latitude, where each point represents the average score of spiders from each city sampled across the expansion gradient. Given the northern expansion of these spiders, latitude is a proxy for distance from the core (Homestead) and colonization history. Green triangles indicate western spiders, whereas purple triangles indicate eastern spiders. The shaded area show the 95% confidence interval for the core population, and the points representing the newest eastern sites are lower than this interval. Inset: Overall, spiders from the eastern population had a lower mean tiptoe latency than those from the western and core populations, driven by patterns at the leading edge.

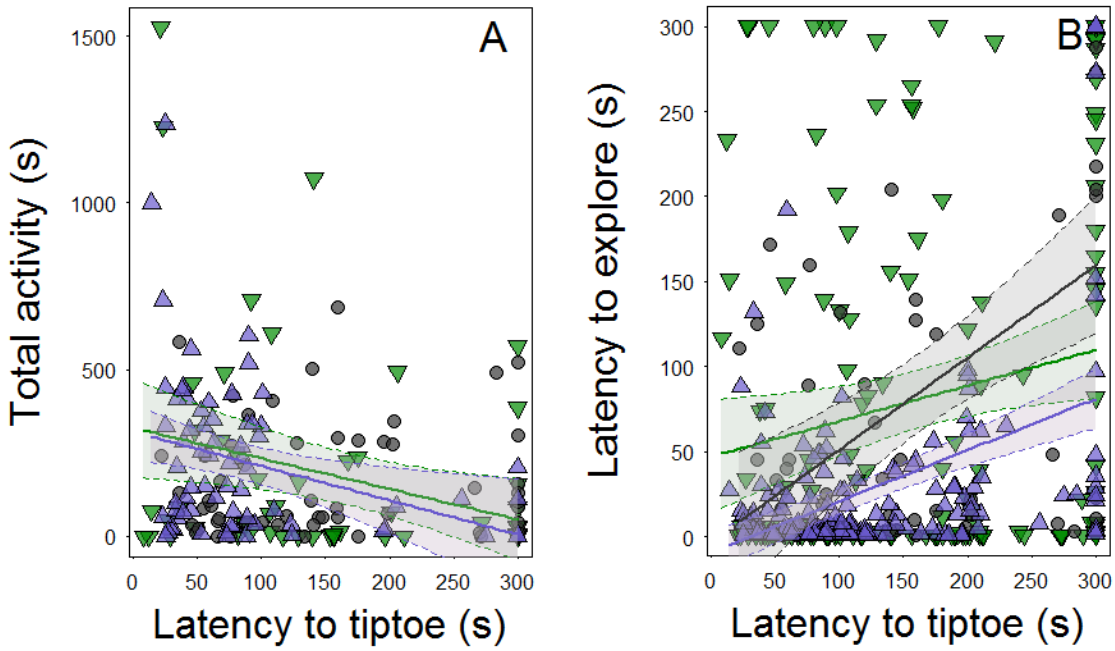

Figure 9. Dispersal syndromes

Green triangles show the western population, purple triangles show the eastern population, and black points show the core population. Shaded areas denote each population's 95% confidence intervals around the line of best fit, if the behavioral correlations were significant. A) In the eastern and western populations, faster dispersing spiders are also active for longer periods. B) Faster dispersing spiders also tend to explore novel environments earlier.

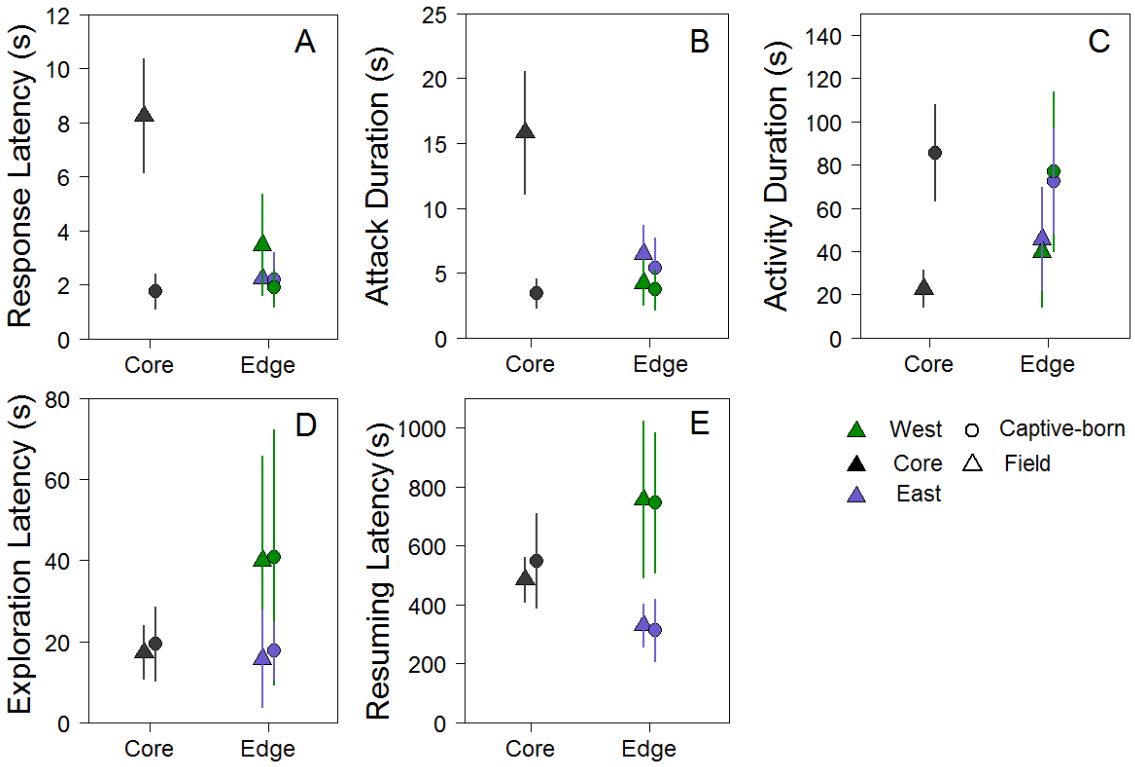

Figure 10. Comparing mean field responses to common garden responses

A) Response latency to prey stimuli, B) attack duration towards prey, and C) activity duration in a novel environment appear to be plastic responses, since individuals raised in standard laboratory conditions converged on similar means, and differences between core and leading edges detected among individuals in the field were not found. In contrast, patterns of core and edge differences in individual latencies D) to explore a novel environment and E) resume activity after a predator stimulus were retained in common garden spiders, suggesting a heritable component to these behaviors.

CHAPTER IV
COMPARING PERSONALITIES BETWEEN NATIVE AND NON-NATIVE POPULATIONS OF *CYRTOPHORA CITRICOLA*

Abstract

Non-native populations can differ from their native counterparts due to various selective processes filtering out certain phenotypes at various stages of invasion. Under this paradigm, phenotypes in introduced populations may represent non-random subsets of their native population that promote colonization and invasion success. Since behavior mediates individual responses to novel environments, we hypothesized that personality traits related to invasion success, including increased aggression, exploration, activity, and boldness, will be more common in species' non-native ranges than native ones. We tested this in the invasive orbweaver, *Cyrtophora citricola*, by comparing two native populations from Spain and South Africa with non-native ones in Florida. The non-native core population in Florida did not differ from native South African populations in any behaviors, and were also behaviorally more similar to native Spanish populations than spiders at the leading edges of its invasion fronts. Our measurements of spider personality traits from the native ranges also served as null models to compare our previous findings of strong behavioral clines occurring along a northward latitudinal expansion gradient in *C. citricola*'s non-native Florida range. We found that latitude predicted few behavioral patterns in the native ranges, suggesting that the behavioral clines in Florida are due to range expansion processes instead of the transportation, introduction, and establishment phases. Overall, we did not find support for personality trait shifts in the non-native range due to selection processes occurring along the introduction pathway. Instead, range expansion processes like spatial sorting may be responsible for higher behavioral variation within the non-native range than variation between non-native and native ranges.

Introduction

Within the last two centuries, humans have drastically improved our speed and ability to move species around the globe, both intentionally and unintentionally. This has, in turn, increased opportunities for biological invasions to occur (Jenkins 1996, Levine and D'Antonio 2003). Nonetheless, the increasing incidences of species introductions may belie the fact that only a small proportion of cases lead to the establishment and spread of non-native species outside of their introduced range (Drake et al. 1989, Williamson 2006).

In order to be invasive, a species needs to overcome each of four stages—transportation, introduction, establishment, and spread (Williamson 1996, Blackburn and Duncan 2001, Blackburn et al. 2011). First, it must move to or be picked up by a vector of transportation (e.g. a commodity being shipped). It

must also survive the transportation process, which can include biosecurity measures such as screening, quarantine, or disinfection (Meyerson and Reaser 2003). Secondly, it must survive in a foreign environment outside of its native geographic range. Thirdly, individuals must find conspecifics to successfully reproduce with. Lastly, the species may spread from the initial core establishment area.

A host of biogeographical, ecological, evolutionary, demographic, and socioeconomic factors affect the probability of individuals bypassing these stages (Williamson 2006, Blackburn et al. 2015). These stages can act as a selective filter to weed out individuals from an initial introduced group. In the case of unintentional introductions, some individuals may be detected during transportation, or simply not survive the duration of transportation under limited space, water, food, or proper shelter (Wonham et al. 2001). Others simply may not survive in an introduced range due to experiencing different abiotic factors outside of their physiological capabilities or biotic interactions outside of their evolutionary history. As such, invasion biologists recognize that not only do successful invaders comprise a non-random subset of all species (Crawley et al. 1996, Daehler 1998, McKinney and Lockwood 1999), but the founding individuals of invading populations may have specific characteristics that predispose them for success over others of the same species (Carere and Gherardi 2013).

The potential role of behavior in successful invasions has been increasingly recognized (Holway and Suarez 1999, Sol et al. 2002, Weis 2010, Chapple et al. 2012, Carere and Gherardi 2013, Hudina et al. 2014). Many studies have compared invasive species with native congeners to identify suites of behaviors that promote invasiveness (Dick et al. 1995, Pintor et al. 2008, Blight et al. 2017, Pradabphetrat et al. 2017), finding differences in neophobia, aggressiveness, and voracity in invasive species. However, much more remains to be known on how intraspecific behavioral variation contributes to successful invasions (Chapple et al. 2012). Animal personalities describe intraspecific behavioral differences that remain consistent over time (Gosling 2001, Sih et al. 2004). A wide variety of both vertebrate and invertebrate taxa, including spiders (Hedrick and Riechert 1989, Pruitt et al. 2008, Pruitt et al. 2011, Grinsted et al. 2013), are known to possess personalities. This means that populations are often comprised of individuals that vary along continuums of traits such as aggression, boldness, and neophilia.

Given the selective filters present in the various stages of invasion, certain personality types may be more likely to persist and become successfully established in a new range (Chapple et al. 2012, Juette et al. 2014). The composition of establishing individuals may thus represent a non-random sample from the group initially transported (Figure 11). For instance, Chapple et al. suggest that bolder, and more exploratory/active individuals are more likely to become stowaways with shipping cargo (2012). Certain heritable behavioral phenotypes may even be lost at certain stages of invasion (e.g. neophobic,

unexploratory individuals incapable of escaping from a cargo hold), leading to founder effects in the introduced range. Higher levels of aggression can aid in species establishment, especially if it allows them to outcompete and displace native congeners (Duckworth and Badyaev 2007, Chucholl et al. 2008, Pintor et al. 2008). Bolder and exploratory individuals may exploit novel habitats and resources better than shy ones (Martin and Fitzgerald 2005, Short and Petren 2008). Studies comparing native and non-native populations of the same species are thus necessary to understand how the various selective filters associated with invasion may shape the phenotypic composition of non-native populations (Felden et al. 2018).

The presence of multiple native and non-native populations of the spider *Cyrtophora citricola* (Forskål 1775) offers the opportunity to understand how personality types vary in both population types. We previously reported that across the subsequent range expansions in the non-native range, *C. citricola* spiders showed behavioral clines, with more active and more aggressive personality types at the leading edges of two expanding populations (Chapter 2). Since higher levels of aggression, exploration, and boldness are also linked to invasion success (Martin and Fitzgerald 2005, Pintor et al. 2008, Liebl and Martin 2012, Hudina et al. 2014), we predicted that 1) spiders from the core established population in Florida would be bolder, more exploratory, and more aggressive than those from their native populations in Spain and South Africa, and that 2) population-level compositions of personality would vary more between non-native and native populations than within them.

We further treated the native populations as null models to test whether the latitudinal clines in behavior observed in the non-native populations also occur in the native populations, which we assumed would be free of underlying range expansion processes that could account for behavioral patterns observed in the non-native ranges. We hypothesized that while mean personality types might vary across the range due to local adaptation to specific environmental differences across sites, that 3) overall latitudinal differences in personalities would not be present in the native range, as they are in the non-native range.

Methods

Introduction and natural history of study organism

Cyrtophora citricola is a facultatively colonial spider with a broad native range, including the Mediterranean, Middle East, Africa, and Asia (Blanke 1972, Levi 1997). Despite multiple unintentional introductions into the Americas and Caribbean within the last 25 years (Levi 1997, Alayon Garcia et al. 2001, Starr 2005, Edwards 2006, Viquez 2007), it is unclear where the spiders are being introduced from. The Mediterranean region and southern Africa are two hypothesized origins due to high volumes of maritime commercial trade between these regions and the Americas (Segura Hernandez 2019), as well as

preliminary molecular analyses from samples across both non-native and native ranges (Ren-Chung Cheng, unpublished data). Given the uncertainty around this topic, we treat both Spain and South Africa as potential source locations for the introduced populations of *C. citricola* in Florida.

The exact introduction pathway of this spider also remains unknown. Many initial discoveries of *C. citricola* are on ornamental trees, fruit orchards, and crop plantations, as well as in manmade habitats (Alvares and De Maria 2004, Edwards 2006, Viquez 2007, Elverici et al. 2012). The major pathways for spider introductions are from fruit shipments, potted plants, or from packaging material and containers associated with the global shipping industry (Nentwig 2015), and some have speculated that *C. citricola* is being introduced with plant imports (Alvares and De Maria 2004, Segura Hernandez 2019). Notably, the core population in Florida is in the city of Homestead, located in Miami-Dade County. This area has the largest plant nursery industry in Florida and over 1400 tropical fruit farms (www.dade-agriculture.org), which supports the idea that the spiders may have been imported from their native range with horticultural or agricultural products.

While its ecological effects on its introduced community remains unclear, *C. citricola* is considered a pest in citrus and coffee plantations (Cárdenas-Murillo et al. 1997, Alayon Garcia et al. 2001, Serra et al. 2003, Serra 2005). The observation that small tree or branch death can occur after the establishment of large colonies on these plant substrates has created speculation that the dense, silken webbing may "asphyxiate" trees (Levi 1997, Alayon Garcia et al. 2001, Edwards 2006, Martin-Castejon and Sanchez-Ruiz 2010). Some believe that the webs absorb and retain solar radiation, causing young leaves and fruits to wither within, although no empirical evidence of these processes exist yet (Cárdenas-Murillo et al. 1997). In addition to potentially preventing photosynthesis, this dense webbing creates physical and psychological difficulties for coffee plantation workers who need to reach into these webs to harvest fruits (Cárdenas-Murillo et al. 1997).

Field behavioral assays

We assayed spiders from 3-5 sites in each of four cities across two populations in Florida, USA (collection details reported in Chapters 2 and 3). These populations have branched from Homestead, where *C. citricola* initially established in Florida. As such, we considered Homestead to be the core population in Florida, and the eastern and western populations represent newer sites that this species has spread to, encompassing the current invasion fronts.

We also assayed spiders in the same design from five cities in Spain and South Africa (Table 15; Figure 12). Whereas the non-native populations were sampled along their existing 2-3 degree latitudinal gradient, we chose greater latitudinal gradients from the native range to better understand the effects of

latitude on phenotypic distribution of *C. citricola* (5 degrees in Spain, 8 degrees in South Africa).

From 26 May to 16 June, 2016, we assayed 578 *C. citricola* from across their range in Spain. Since they occur along coastal Spain (Cardoso and Morano 2010), we assayed between 68-152 individuals per locality at Girona, Valencia, Murcia, Malaga, and Cadiz. There were notably fewer individuals (n=68) found at the northernmost city, Girona.

From 9 March to 31 March, 2017, we assayed 656 *C. citricola* from their South African range (Table 15; Figure 12). Given the drought at the time (worldweatherattribution.org), we chose locations where they were known to be present (Charles Haddad, personal communication). We measured between 73-206 individuals per locality at Port Elizabeth, Cradock, Bloemfontein, Klerksdorp, and Zeerust.

In their non-native range, *C. citricola* are common in urban habitats and found abundantly on manmade metal substrates like guard rails, bridge rails, and street signs (Chapter 2). In contrast, we primarily found these spiders on sturdy non-native plant substrates, such as *Opuntia* sp., *Cylindropuntia* sp., *Yucca* sp., and *Agave americana* in Spain (Chuang and Leppanen 2018) as well as South Africa. We assayed *C. citricola* for foraging aggression directly on their web substrates before individually collecting them and bringing them into a climate-controlled, indoor location to test for bold and exploratory behaviors in novel environments. All spiders were tested within five hours of capture, and assaying equipment was cleaned with ethanol between each trial to reduce any chemical or olfactory cues.

In total, we measured five behaviors of interest in the field (further details in Chapters 2 and 3):

To measure foraging aggression, we simulated prey struggling in a web by electronically vibrating the edge of an individual's web. We subsequently timed the latency for the spider to respond, whether or not they responded to the stimulus, the total duration of the attack (the difference between the total length of the assay and the latency to respond), and whether or not they attacked the stimulus with a bite within two minutes.

To measure the exploration and activity of an individual, we introduced a spider into a plastic arena and timed the latency for the spider to initiate activity, whether or not activity was initiated within a five minute trial period, and the total duration of activity inside the arena.

To measure the boldness of an individual, we delivered two sharp gusts of air with a rubber bulb to each individual in the plastic area, to stimulate the approach of an avian predator. All individuals responded with an expression of thanatosis, a frozen "huddle" posture. We measured the latency for individuals to resume a normal posture and activity after the puffs of air, and whether or not they did so within a 60 minute timeframe.

Statistical Methods

We analyzed all data in R (R Core Team 2013). To determine whether different populations (e.g. Spanish, South African, core, eastern, and western) varied significantly from each other, we analyzed data from all of the spiders together (n = 2430). We used logistic regression models to analyze binomially-distributed behavioral responses; these included "responding to prey stimuli", "completing an attack", "initiating exploration", or "resuming activity after a predatory stimulus". We used negative binomial regression models to determine whether population predicted the latency or duration of our behaviors of interest. We used separate individual models for the Spanish and South African datasets to test whether latitude predicted these behaviors. We included sex and length in the full models, as these traits commonly influence behaviors. Since we could not sexually differentiate spiderlings that were under 3 mm in body length, these were coded as "unknown", and we included this category as well as "male" and "female" for this variable. AIC selection criterion was used for model selection. We used Tukey HSD tests for pairwise comparisons between populations (Spain, South Africa, Florida core, western Florida, eastern Florida).

Results

Population-level comparisons

We did not find evidence of major differences in mean personality scores occurring between native and non-native populations (Table 16 and 17; Figure 12). We did find that Spanish and South African *C. citricola* spiders were more likely to respond to prey stimuli than the spiders from the Florida populations (Table 17; Figure 13). We also found that contrary to our predictions, the core spiders from their non-native range actually resembled the native population spiders more than the eastern and western spiders. They were as likely to attack a prey stimulus and explore as Spanish and South African spiders. Furthermore, our negative binomial models also showed no differences between the South African and Florida core population in any measured latencies or durations of behaviors (Table 18 and 19). Core *C. citricola* were faster to attack a prey stimulus ($\bar{x}$ = -0.4494, 95% CI = (-0.8680, -0.03077), p = 0.0284) compared to Spanish spiders. In contrast, spiders from the western and eastern populations in Florida differed from the core population in most of the behavioral measurements, driven by diverging personality composition at the leading edge of these two populations (Table 17 and 19; reported in Chapter 2).

Latitudinal effects

We did not find strong effects of latitude on behaviors in our individual models of the Spanish and South African populations (Table 20 and 21, Figure

14 and 5). Spanish *C. citricola* alone were more active at higher latitudes ($F = 5.513$, $df = 1$, $p < 0.0001$). None of the measured behaviors showed latitudinal clines for the South African population.

Discussion

We found few behavioral differences between the native *C. citricola* populations and the Florida core population, which is the initial establishment point of these spiders in Florida. While the core spiders were less likely to respond to prey stimuli, they were also more likely to initiate activity after a predatory stimulus. Neither core nor Spanish population individuals differed significantly from the South African one in any behavioral measures. However, Spanish *C. citricola* were less aggressive and less bold than core spiders in Florida. The Spanish population showed some latitudinal differences in behavior, with fewer spiders that attacked prey stimuli at higher latitudes and more active individuals at higher latitudes. However, the South African population, which spanned over a greater latitudinal gradient than in Spain, did not show any latitudinal clines in behavior. As such, it seems unlikely that all of the behavioral clines we previously observed in Florida are solely due to the 2-3 degree latitudinal gradient that they have spread across.

We found that despite being less likely to react to prey in their webs, core spiders that did so were faster than Spanish spiders to attack prey. Quick response times are relevant for prey capture in *C. citricola* spiders, because they use non-sticky silk in their webs. Instead of adhering to sticky webbing, prey tend to become trapped in a dense array of vertically-oriented silk strands that are found at the top of the tent-shaped web of these spiders (Rypstra 1979). Entangled prey may fall into the horizontal orb web below these strands, where the spiders sit. However, there is no guarantee that this will occur. Prey may successfully detangle themselves and escape if the spiders do not shake the web, causing them to fall into the orb web, or run and subdue them by biting and wrapping them in silk. As such, spiders with lower latencies to attack prey often capture more prey (Costa-Pereira and Pruitt 2019), which may allow them to catch novel prey and persist in new environments.

We also found that core spiders were more likely than native *C. citricola* to resume activity within an hour of being exposed to a predator cue, a strong puff of air. This stimulus resembles the approach of an avian predator (Riechert and Hedrick 1993), and causes about 99% of *C. citricola* to immobilize in a huddled posture and possibly feign death. Despite anecdotal accounts of birds attacking spider colonies in the native range (Wheeler 1926), we never observed any predation events in the non-native range. Given the roadside urban environments that *C. citricola* is found in, it is unclear what forms of predation pressure these spiders face. If natural enemies are rarer in the introduced range of these spiders, especially in the urban habitats that they are found in, it is possible that

bolder spiders are not selected against during the establishment and range expansion stages of this spider's invasion. If anything, risk-taking individuals may better exploit resources, especially in manmade environments (Short and Petren 2008).

Despite this, we found no evidence of selective filters present at the transportation, introduction, and establishment phases of their invasion that have reduced phenotypes present in the non-native range and shifted mean personality types accordingly. This differs from other known cases where a species experienced a population bottleneck during introduction (Tsutsui et al. 2000). For instance, the success of the Argentine ant (*Linepithema humile*) invasion has been attributed to reduced genetic diversity in non-native populations leading to lower intraspecific aggression, lowered conflict between conspecific colonies, and higher worker densities with which to compete against native ant species (Suarez et al. 1999, Tsutsui et al. 2000, Blight et al. 2017).

We additionally found that the core population was more behaviorally similar to the South African population than it was to the Spanish population. Segura Hernandez (2019) suggests that southern Africa is a more likely origin than the Mediterranean of the introduced *C. citricola* populations of the Americas. This conclusion is based on ecological niche model analyses showing that invasive *C. citricola* populations from the Americas and Caribbean (including USA, Cuba, Brazil, Costa Rica, Colombia, Dominican Republic, Haiti) occur in environments more similar to the southern African region than the Mediterranean region. In addition, preliminary molecular analyses based on the CO1 gene suggest that the non-native populations are more related to *C. citricola* from South Africa than specimens collected from Madagascar, Malaysia, Israel, or Spain (Ren-Chung Cheng, unpublished data). The greater behavioral similarity between core Florida spiders and South African spiders may lend support to the hypothesis that South Africa is the origin of these spiders. However, we favor a cautious interpretation of our study in this context, since it is also possible that similar selective forces from similar environments may convergently shape plastic personality traits.

The apparent lack of personality shifts from overcoming various invasion stages may be due to several factors. First, it is possible that the transportation phase imposes few barriers for specific behavioral phenotypes. This is likely if the spiders are on vectors like potted horticultural or agricultural plants that preserve a suitable microhabitat for them, as opposed to an agricultural product that must be picked, processed, packaged, and placed into a shipping container (e.g. fruits). Lax biosecurity processes may also fail to detect or exterminate small spiderlings that can create inconspicuous webs on plants and shipping materials. If *C. citricola* egg sacs escape detection on potted plants and saplings, then there might be little to no selection on individual phenotypes.

Secondly, *C. citricola* may possess physiological characteristics that can tolerate the stresses associated with transportation and introduction. The

duration of transportation for cargo from Africa and the Mediterranean to the United States ranges between one to three weeks, which may not be long enough to impose strong stressors on individuals. In our field studies from Florida, we found that nearly all smaller spiderlings (< 6 mm in body length) survived with no food and occasional water misting during periods lasting up to 18 days from field capture to introduction in laboratory conditions (Chuang, personal observation). The high survivorship from integrating wild-caught individuals to laboratory conditions, as well as our ability to easily raise spiderlings from wild-caught egg sacs suggests that this species may adapt well to novelty and different environmental conditions, further explaining their nearly global distribution spanning different habitats. If this species has the physiological capabilities to weather the stresses associated with their introduction pathway, then selection also will not occur. Our observations of their ability to survive with infrequent feeding and watering invites future studies on the role that metabolism and physiology can play in *C. citricola*'s invasion success.

The lack of behavioral differentiation between the native and non-native ranges can also be explained by the plasticity of behavioral phenotypes. We previously showed that of our five behavioral traits of interest, prey response latency, attack duration, and activity duration are plastic personality traits. While these traits showed repeatability in individuals (Chapter 2), rearing conditions seem to influence the development of these personality types. We previously found that most laboratory-raised spiders were quick to respond and attack prey stimuli, and population-level differences failed to emerge in a common garden environment (Chapter 3). Thus, phenotypic plasticity can explain why foraging and activity personality types may not change despite selective filtering of certain genotypes at various stages of invasion.

However, the environmental and ecological dissimilarities between the native and non-native ranges make it less likely that the personality types of the native and non-native range have converged by random chance or plastic responses to their environment. Florida is characterized by tropical and subtropical climate, and on average *C. citricola* experience between double to triple the amount of rainfall as well as 5°-10° temperatures warmer than those in the native range (Table 1). In contrast, the spiders we tested *in situ* in Spain and South Africa were in dry summer and arid climate types and generally collected from large, succulent plants, unlike the metal substrates favored by Florida *C. citricola*. Also, *C. citricola* eggs are parasitized by egg predators in the wasp genus *Philolema* in both Spanish (Chuang et al., 2019) and South African (Chuang, unpublished data) ranges. *Philolema palanichamyi* emerged from approximately 40 % of egg sacs collected across the Spanish range. In contrast, no egg parasitoids or associates have ever emerged from egg sacs we collected in Florida from 2014-2017, suggesting that these wasps have not been introduced to the non-native ranges yet. Despite differences in climate, habitat,

web substrates, and natural enemies, there is more behavioral variation within the expanding range than between the non-native core and native populations.

A unifying factor between the native populations and the core population is that they are not subject to the range expansion processes that characterize newer sites along the eastern and western populations of Florida. Instead of more dispersive individuals expanding range boundaries to new areas of suitable habitat, range edges at the native range likely represent population sinks where population growth is close to zero (Bridle and Vines 2007). It is possible that the relatively static nature of these populations have led to a convergence of similar personality types in different populations. This contrasts with the dynamic nature of the expanding eastern and western population in Florida, where spatial sorting appears to underlie some behavioral shifts and account for more dispersive, exploratory, and active spiders in the eastern population (Chapter 3). Since spatial sorting can result in patterns similar to runaway selection, where rare alleles can surf through repeated founder effects, phenotypic composition at the edge is subject to turnover. This means that range expansions can create ephemeral phenotypic patterns through space (Chuang and Peterson 2016), and the rate of turnover likely depends on how locally adaptive leading edge phenotypes are. If this is true, then it is possible that some of the current behavioral patterns observed at the invasion fronts of *C. citricola* in Florida will be subject to other selective forces besides spatial selection. Given the behavioral similarities of the core population to native populations, despite environmental and ecological differences, we might expect the current range fronts to also resemble personality compositions of the native population over time.

In conclusion, we did not detect any evidence of selective filtering of personality types occurring during the transportation, introduction, and establishment phase of *C. citricola*'s invasion in Florida. Instead, the differences between the core and leading edges of this spider's non-native ranges were greater than between the core and the native Spanish and South African ranges. Given that our measured behaviors were generally not assorted by latitude across the native ranges, we cannot rule out the role of spatial sorting in assorting personality types across the non-native range. As such, our study shows that population-level personality traits in a species can remain stable across transportation, introduction, and establishment phases in invasions. Instead, it is the spreading phase of invasion that may rapidly change the distribution of personalities through space.

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Appendix D

Table 15. Sampling locations from *C. citricola*'s native and non-native range

We include major cities, GPS coordinates, sample sizes, as well as climate descriptions, including average temperature and annual precipitation from climate-data.org.

Locations	Population	Latitude	Longitude	Avg temp (°C)	Rainfall (mm)	Köppen climate type	Climate description	Sample size	Native status	Assay Periods
Homestead	Core - Florida	25.50736	-80.47782	23.6	1534	Aw	Tropical wet and dry	282	Non-native	July 2015, August 2017
Fort Lauderdale	East - Florida	26.15787	-80.16132	24.0	1528	Af	Equatorial fully humid	99	Non-native	July 2015
West Palm Beach	East - Florida	26.14125	-80.06764	23.6	1497	Am	Tropical monsoon	109	Non-native	July 2015
Fort Pierce	East - Florida	27.42947	-80.37226	22.9	1321	Cfa	Humid subtropical	63	Non-native	July 2015
Vero Beach	East - Florida	27.64523	-80.39852	22.8	1305	Cfa	Humid subtropical	113	Non-native	July 2015
Naples	West - Florida	26.14498	-81.76094	23.4	1303	Aw	Equatorial winter dry	123	Non-native	August 2017
Fort Myers	West - Florida	26.61877	-81.94351	23.2	1348	Cfa	Humid subtropical	137	Non-native	August 2017
Sarasota	West - Florida	27.33594	-82.49768	22.4	1328	Cfa	Humid subtropical	130	Non-native	August 2017
Clearwater	West - Florida	28.12911	-82.77115	22.2	1266	Cfa	Humid subtropical	169	Non-native	August 2017
Girona	Spain	41.67076	2.78615	15.4	729	Csa	Dry summer	68	Native	May 2016

Table 15 Continued

Locations	Population	Latitude	Longitude	Avg temp (°C)	Rainfall (mm)	Köppen climate type	Climate description	Sample size	Native status	Assay Periods
Valencia	Spain	39.82966	-0.47370	17.4	445	Csk	Cold semi-arid	152	Native	June 2016
Murcia	Spain	37.87013	-1.14215	18.1	293	Csh	Arid steppe hot arid	109	Native	June 2016
Malaga	Spain	36.73705	-4.40486	18.4	520	Csa	Dry summer	120	Native	June 2016
Cadiz	Spain	36.32299	-5.88251	17.9	597	Csa	Dry summer	129	Native	June 2016
Port Elizabeth	South Africa	-33.91719	25.10931	17.4	561	Bsh	Oceanic climate	104	Native	Mar 2017
Cradock	South Africa	-32.05031	25.37501	16.6	338	Bsk	Cold semi-arid	73	Native	Mar 2017
Bloemfontein	South Africa	-29.11102	26.18685	16.1	548	Bsk	Cold semi-arid	206	Native	Mar 2017
Klerksdorp	South Africa	-26.89295	26.64636	17.0	603	Bsk	Cold semi-arid	137	Native	Mar 2017
Zeerust	South Africa	-25.55180	26.10621	18.5	583	Bsh	Arid steppe hot arid	135	Native	Mar 2017

Table 16. Logistic regression model outputs in behavioral frequency across populations

Outputs from our best logistic regression models predicting the frequency of spiders responding to prey stimuli, attacking prey stimuli, exploring a novel arena, and resuming activity after a predator stimuli to population, length, and sex.

Model for spiders responding to prey stimuli (n = 2274)			
Predictors	*df*	χ^2	p-value
Intercept	1	61.0877	< 0.0001
Population	4	56.2966	< 0.0001
Sex	2	11.8818	0.0026
Length	1	5.6123	0.0178
Model for spiders attacking prey stimuli (n = 2276)			
Predictors	*df*	χ^2	p-value
Intercept	1	20.4892	< 0.0001
Population	4	51.0941	< 0.0001
Sex	2	5.4432	0.0658
Length	1	11.8075	0.0006
Model for spiders exploring in a novel arena (n = 2332)			
Predictors	*df*	χ^2	p-value
Intercept	1	31.7876	< 0.0001
Population	4	158.4981	< 0.0001
Sex	2	5.6499	0.0593
Length	1	20.661	< 0.0001
Model for activity after a predator stimulus (n = 2337)			
Predictors	*df*	χ^2	p-value
Intercept	1	63.9886	< 0.0001
Population	4	134.6542	< 0.0001
Sex	2	3.0211	0.2208

Table 17. Tukey HSD pairwise contrasts in binomially-distributed behaviors across all populations

Tukey HSD pairwise contrasts between binomially-distributed behaviors across different populations in the native and non-native ranges. Bolded pairs indicate significant differences in each behavior.

Spiders responding to prey stimuli (n = 2274)				
Population Comparisons	Difference	Lower CI	Upper CI	p-value
South Africa-Core	0.0840	0.0143	0.1537	0.0089
Spain-Core	0.1053	0.0353	0.1753	0.0004
East-Core	0.0072	-0.0716	0.0861	0.9991
West-Core	-0.0191	-0.0894	0.0513	0.9470
Spain-South Africa	0.0212	-0.0315	0.0740	0.8072
East-South Africa	-0.0768	-0.1409	-0.0127	0.0096
West-South Africa	-0.1031	-0.1564	-0.0498	< 0.0001
East-Spain	-0.0980	-0.1625	-0.0336	0.0003
West-Spain	-0.1243	-0.1780	-0.0707	0.0000
West-East	-0.0263	-0.0912	0.0385	0.8022
Spiders attacking prey stimuli (n = 2276)				
Population Comparisons	Difference	Lower CI	Upper CI	p-value
South Africa-Core	-0.0094	-0.1118	0.0929	0.9991
Spain-Core	-0.0075	-0.1104	0.0953	0.9996
East-Core	0.1755	0.0597	0.2914	0.0004
West-Core	0.0937	-0.0096	0.1971	0.0965
Spain-South Africa	0.0019	-0.0757	0.0795	1.0000
East-South Africa	0.1850	0.0908	0.2792	< 0.0001
West-South Africa	0.1032	0.0249	0.1814	0.0030
East-Spain	0.1831	0.0884	0.2778	< 0.0001
West-Spain	0.1013	0.0224	0.1801	0.0042
West-East	-0.0818	-0.1771	0.0134	0.1312
Spiders exploring in a novel arena (n = 2332)				
Population Comparisons	Difference	Lower CI	Upper CI	p-value
South Africa-Core	0.0873	-0.0067	0.1813	0.0832
Spain-Core	-0.0290	-0.1241	0.0661	0.9207
East-Core	0.1983	0.0931	0.3035	< 0.0001
West-Core	-0.1835	-0.2789	-0.0881	< 0.0001
Spain-South Africa	-0.1163	-0.1904	-0.0422	0.0002
East-South Africa	0.1110	0.0243	0.1977	0.0044
West-South Africa	-0.2708	-0.3453	-0.1963	< 0.0001
East-Spain	0.2273	0.1394	0.3151	< 0.0001
West-Spain	-0.1545	-0.2304	-0.0786	< 0.0001
West-East	-0.3818	-0.4700	-0.2936	< 0.0001

Table 17 Continued

Spiders resuming activity after a predator stimulus (n = 2337)				
Population Comparisons	Difference	Lower CI	Upper CI	p-value
South Africa-Core	-0.2754	-0.3695	-0.1813	< 0.0001
Spain-Core	-0.1359	-0.2311	-0.0407	< 0.0001
East-Core	0.0883	-0.0164	0.1931	0.1444
West-Core	-0.1264	-0.2217	-0.0311	0.0028
Spain-South Africa	0.1395	0.0649	0.2141	< 0.0001
East-South Africa	0.3637	0.2773	0.4502	< 0.0001
West-South Africa	0.1490	0.0743	0.2237	< 0.0001
East-Spain	0.2242	0.1366	0.3119	< 0.0001
West-Spain	0.0095	-0.0666	0.0856	0.9971
West-East	-0.2147	-0.3025	-0.1270	< 0.0001

Table 18. Negative binomial regression model outputs for all *C. citricola* populations

Negative binomial regression model outputs for all *C. citricola* predicting foraging aggression (latency to attack, attack duration), exploration/activity (latency to explore, total activity), and boldness (latency to resume activity after predator stimulus) as a function of population, sex, and length.

Model for the latency for spiders to respond (n=1980)			
Predictors	*df*	F	p-value
Population	4	6.1451	< 0.0001
Length	1	24.4116	< 0.0001
Model for the attack duration of spiders (n=968)			
Predictors	*df*	F	p-value
Population	4	20.477	< 0.0001
Length	1	1.5605	0.2119
Sex	2	6.8243	0.0011
Model for the exploratory latency in a novel environment (n=1475)			
Predictors	*df*	F	p-value
Population	4	9.5162	< 0.0001
Sex	2	1.3756	0.2530
Model for the total activity duration in a novel environment (n=1382)			
Predictors	*df*	F	p-value
Population	4	4.8383	0.0007
Sex	2	15.1507	< 0.0001
Model for the latency to resume activity after a predatory stimulus (n=1510)			
Predictors	*df*	F	p-value
Population	4	7.2475	< 0.0001
Length	1	21.9223	< 0.0001
Sex	2	6.7511	0.0012

Table 19. Tukey HSD pairwise contrasts in negative binomially-distributed behaviors across all populations

Tukey HSD pairwise contrasts between negative binomially-distributed behaviors across different populations in the native and non-native ranges. Bolded pairs indicate significant differences in each behavior.

Model for the latency for spiders to respond (n=1980)				
Population Comparisons	Difference	Lower CI	Upper CI	p-value
Core-South Africa	0.206058	-0.09207	0.504186	0.32341
Core-Spain	-0.00077	-0.29628	0.294729	1
Core-East	0.2619	-0.08039	0.604187	0.2243
Core-West	0.624954	0.314956	0.934951	<0.0001
South Africa-Spain	-0.20683	-0.42411	0.010452	0.07106
South Africa-East	0.055843	-0.21812	0.329802	0.98099
South Africa-West	0.418896	0.18793	0.649862	<0.0001
Spain-East	0.262674	-0.01201	0.537355	0.06895
Spain-West	0.625727	0.392978	0.858476	<0.0001
East-West	0.363053	0.077635	0.648472	0.00495
Model for the attack duration of spiders (n=968)				
Population Comparisons	Difference	Lower CI	Upper CI	p-value
Core-South Africa	-0.1429	-0.55932	0.27353	0.8822
Core-Spain	-0.4494	-0.86804	-0.03077	0.0284
Core-East	0.69989	0.2566	1.14318	<0.0001
Core-West	0.60933	0.19421	1.02445	<0.0001
South Africa-Spain	-0.30651	-0.62668	0.01367	0.0683
South Africa-East	0.84279	0.49384	1.19173	<0.0001
South Africa-West	0.75223	0.44245	1.06201	<0.0001
Spain-East	1.14929	0.80062	1.49797	<0.0001
Spain-West	1.05874	0.75176	1.36571	<0.0001
East-West	-0.09056	-0.42655	0.24543	0.9479
Model for the exploratory latency in a novel environment (n=1475)				
Population Comparisons	Difference	Lower CI	Upper CI	p-value
Core-South Africa	-0.30916	-0.81314	0.19481	0.44922
Core-Spain	-0.2767	-0.79096	0.23755	0.58221
Core-East	0.22384	-0.30736	0.75504	0.77899
Core-West	-1.0219	-1.57636	-0.46743	<0.0001
South Africa-Spain	0.03246	-0.36601	0.43092	0.99946
South Africa-East	0.533	0.10824	0.95776	0.00574

Table 19 Continued

Population Comparisons	Difference	Lower CI	Upper CI	p-value
South Africa-West	-0.71274	-1.14367	-0.2818	<0.0001
Spain-East	0.50054	0.06424	0.93685	0.01537
Spain-West	-0.74519	-1.19756	-0.29283	<0.0001
East-West	-1.24574	-1.72474	-0.76673	<0.0001
Model for the total activity duration in a novel environment (n=1382)				
Population Comparisons	Difference	Lower CI	Upper CI	p-value
Core-South Africa	0.19427	-0.2386	0.62714	0.73523
Core-Spain	0.02338	-0.41632	0.46308	0.9999
Core-East	0.05386	-0.41321	0.52092	0.99785
Core-West	-0.42293	-0.8898	0.04395	0.09676
South Africa-Spain	-0.17089	-0.48359	0.14181	0.56614
South Africa-East	-0.14042	-0.49233	0.2115	0.81101
South Africa-West	-0.6172	-0.95322	-0.28118	<0.0001
Spain-East	0.03047	-0.32906	0.39	0.99936
Spain-West	-0.44631	-0.79828	-0.09434	0.00493
East-West	-0.47678	-0.86585	-0.08771	0.00743
Model for the latency to resume activity after a predatory stimulus (n=1510)				
Population Comparisons	Difference	Lower CI	Upper CI	p-value
Core-South Africa	-0.20127	-0.56197	0.15943	0.5473
Core-Spain	-0.28473	-0.62474	0.05528	0.1496
Core-East	-0.01178	-0.36724	0.34368	1
Core-West	-0.49728	-0.8439	-0.15065	<0.0001
South Africa-Spain	-0.08346	-0.39282	0.22589	0.948
South Africa-East	0.18949	-0.1352	0.51418	0.502
South Africa-West	-0.29601	-0.60261	0.0106	0.0643
Spain-East	0.27295	-0.03217	0.57807	0.1047
Spain-West	-0.21255	-0.50408	0.07899	0.2709
East-West	-0.4855	-0.79055	-0.18044	<0.0001

Table 20 Logistic regression model outputs from Spain and South Africa

Logistic regression model outputs predicting the frequency of spiders responding to prey stimuli, attacking prey stimuli, exploring a novel arena, and resuming activity after a predator stimuli to city, latitude, length, and sex.

Logistic regression models for *C. citricola* spiders from Spain			
Model for spiders responding to prey stimuli (n = 578)			
Predictors	*df*	χ^2	p-value
Intercept	1	38.2695	< 0.0001
City	4	10.5475	0.0322
Length	1	5.9458	0.0148
Model for spiders attacking prey stimuli (n = 578)			
Predictors	*df*	χ^2	p-value
Intercept	1	5.5296	0.0187
Model for spiders exploring in a novel arena (n = 561)			
Predictors	*df*	χ^2	p-value
Intercept	1	64.5820	< 0.0001
Length	1	46.8460	< 0.0001
Model for activity after a predator stimulus (n = 556)			
Predictors	*df*	χ^2	p-value
Intercept	1	7.8283	0.0051
City	4	22.2811	0.0002
Logistic regression models for *C. citricola* spiders from South Africa			
Model for spiders responding to prey stimuli (n = 604)			
Predictors	*df*	χ^2	p-value
Intercept	1	39.1051	< 0.0001
City	4	7.7464	0.1013
Model for spiders attacking prey stimuli (n = 604)			
Predictors	*df*	χ^2	p-value
Intercept	1	4.8386	0.0278
City	4	30.3212	< 0.0001
Length	1	42.7287	< 0.0001
Model for spiders exploring in a novel arena (n = 619)			
Predictors	*df*	χ^2	p-value
Intercept	1	41.2630	< 0.0001
City	4	23.0130	0.0001
Length	1	20.4880	< 0.0001
Model for spiders resuming activity after a predator stimulus (n = 615)			
Predictors	*df*	χ^2	p-value
Intercept	1	10.0345	0.0015
Sex	2	11.4547	0.0033
Length	1	8.2931	0.0040

Table 21. Negative binomial regression model outputs from Spain and South Africa

Negative binomial model outputs from the Spanish and Southern populations predicting foraging aggression (latency to attack, attack duration), exploration/activity (latency to explore, total activity), and boldness (latency to resume activity after predator stimulus) as a function of city, latitude, sex, and length

Negative binomial models for *C. citricola* spiders from Spain			
Model for the latency for spiders to respond (n=549)			
Predictors	*df*	F	p-value
Length	1	12.046	0.0006
Model for the exploratory latency in a novel environment (n=437)			
Predictors	*df*	F	p-value
City	4	1.4665	0.2121
Length	1	9.8655	0.0018
Model for the total activity duration in a novel environment (n = 437)			
Predictors	*df*	F	p-value
City	4	1.9007	0.1100
Latitude	1	5.513	0.0195
Model for the latency to resume activity after a predatory stimulus (n = 304)			
Predictors	*df*	F	p-value
Length	1	19.656	< 0.0001
Negative binomial models for *C. citricola* spiders from South Africa			
Model for the latency for spiders to respond (n=539)			
Predictors	*df*	F	p-value
Length	1	21.49	< 0.0001
Model for the attack duration of spiders (n = 218)			
Predictors	*df*	F	p-value
Length	1	7.2654	0.0076
Model for the exploratory latency in a novel environment (n = 336)			
Predictors	*df*	F	p-value
City	4	1.2874	0.2741
Length	1	21.535	< 0.0001
Model for the total activity duration in a novel environment (n = 336)			
Predictors	*df*	F	p-value
City	4	5.1572	0.0005
Length	1	4.5755	0.0330
Sex	2	4.539	0.0112
Model for the latency to resume activity after a predatory stimulus (n=350)			
Predictors	*df*	F	p-value
Length	1	2.3893	0.1233
Sex	2	4.0509	0.0184

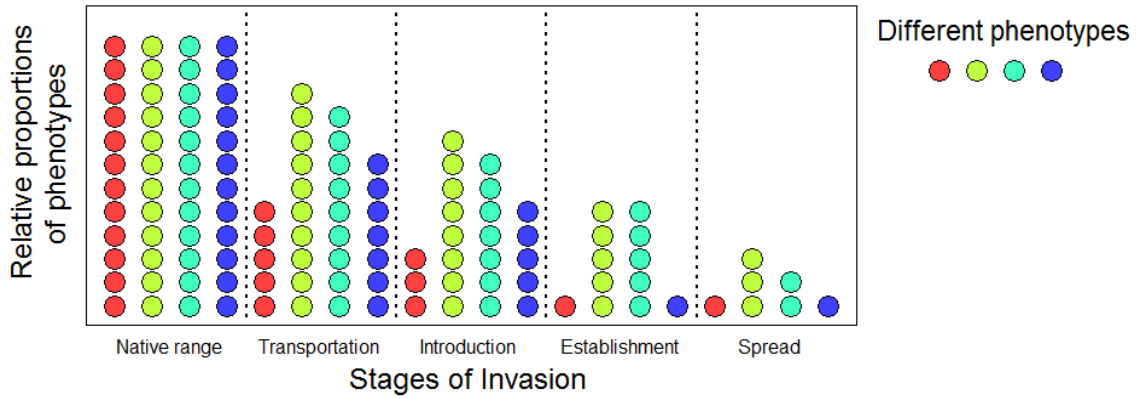

Figure 11. The stages of invasion

The various stages of invasion (transportation, introduction, establishment, spread) may act as selective filters for different behavioral phenotypes, leading to differing proportions of personality types at the non-native range compared to the native range.

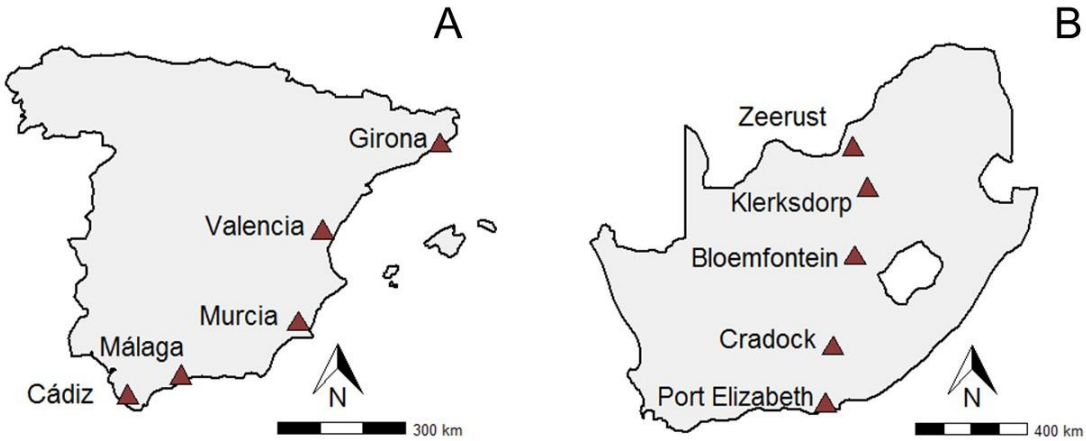

Figure 12. Map of sampling locations in Spain and South Africa

We assayed *C. citricola* around five cities in A) mainland Spain and B) South Africa.

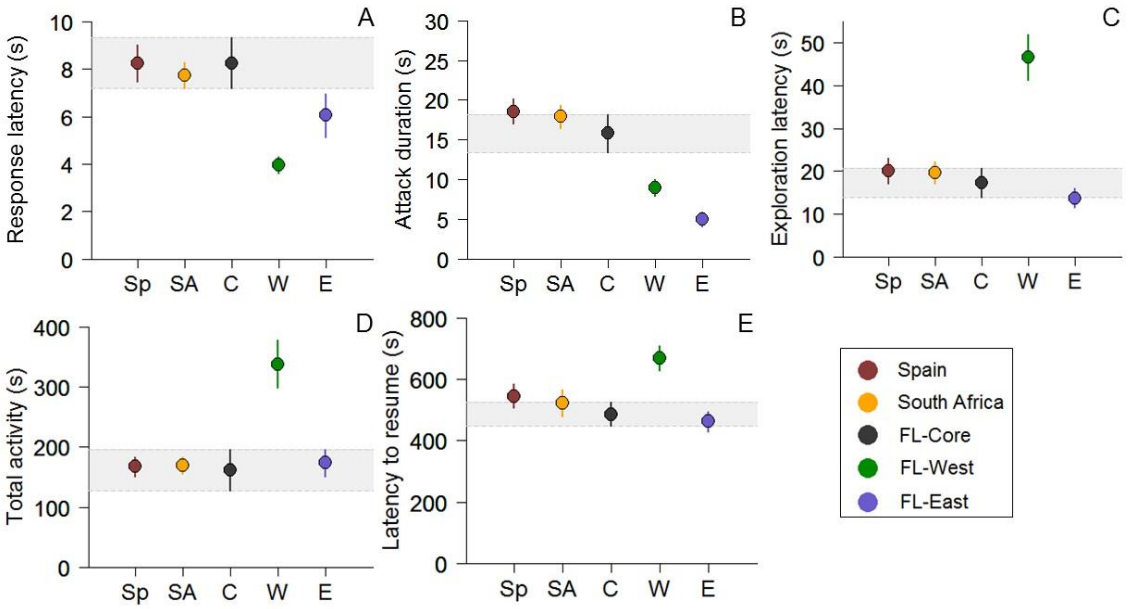

Figure 13. Mean personality scores from each population in the native and non-native range

The shaded area represents the 95% confidence interval for the core population, to offer comparison between the native populations and the non-native populations. “Sp” for Spain, “SA” for South Africa, “C” for Florida core, “W” for Florida western, “E” for Florida eastern population.

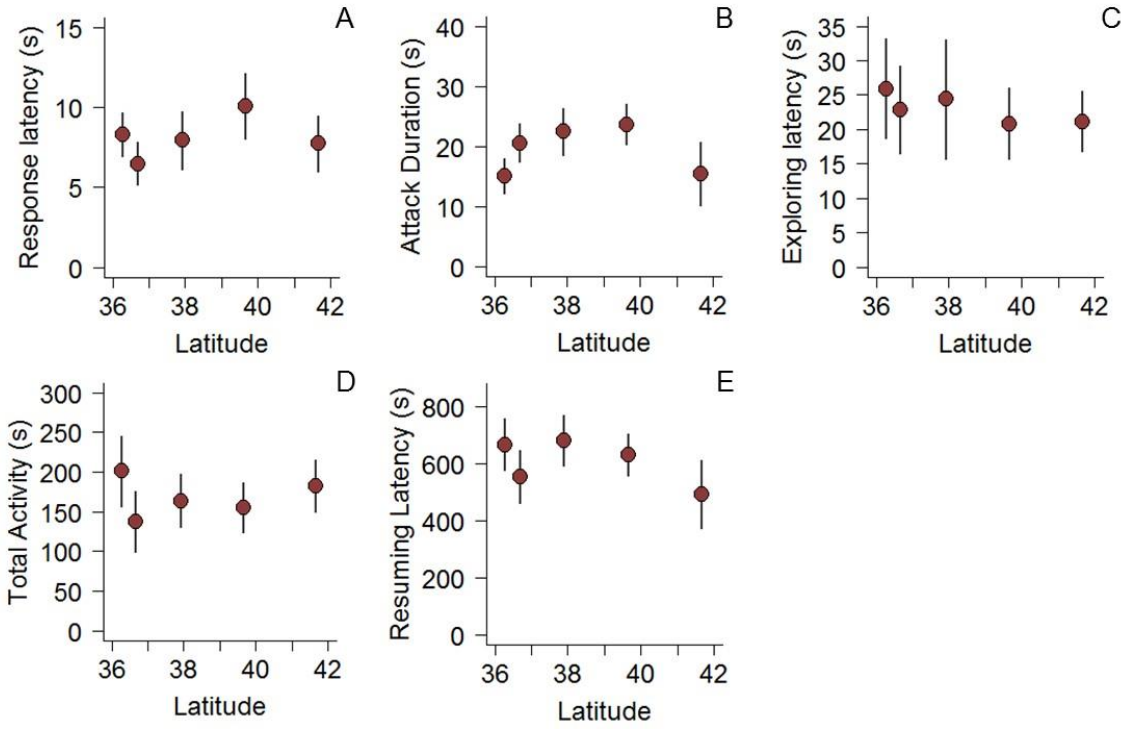

Figure 14. Mean personality scores across latitude in the Spanish population

Mean personality scores with 95% confidence intervals for Spanish *C. citricola* across latitude. Points represent means for spiders from Cadiz, Malaga, Murcia, Valencia, and Girona, from the lowest to highest latitudes.

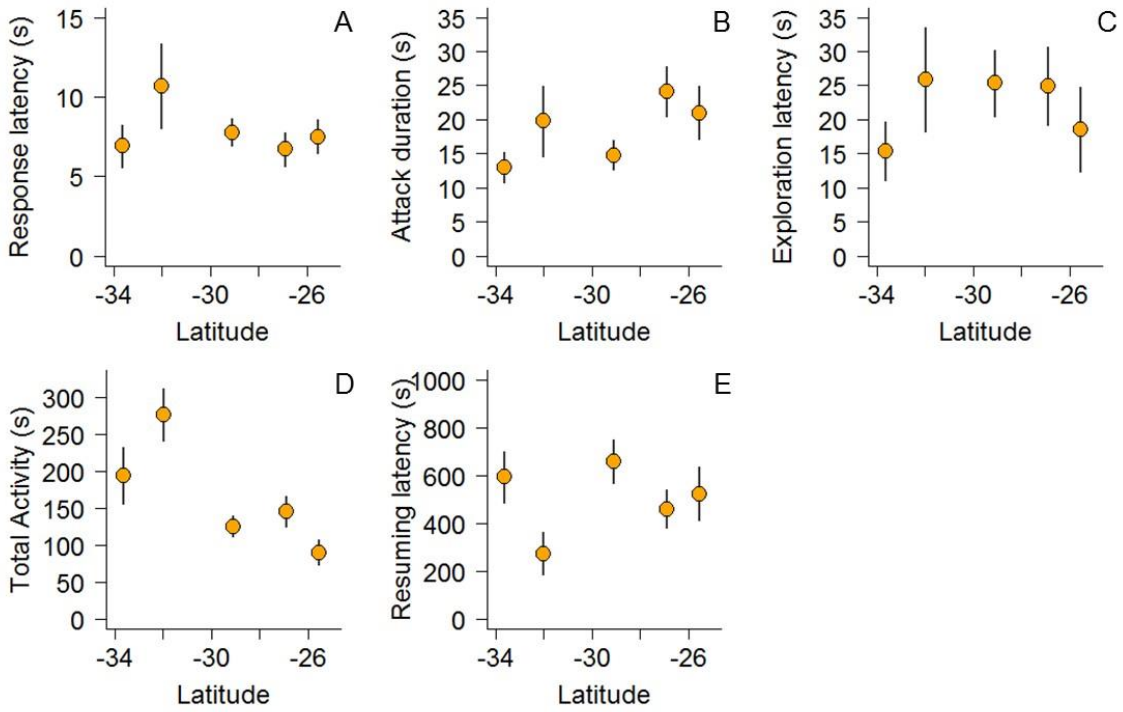

Figure 15. Mean personality scores across latitude in the South African population

Mean personality scores with 95% confidence intervals for South African *C. citricola* across latitude. Points represent means for spiders from Port Elizabeth, Cradock, Bloemfontein, Klerksdorp, and Zeerust from the lowest to highest latitude.

CONCLUSION

In this dissertation, I examined the role of processes underlying different stages of invasion in shaping population-level personality traits, using the recent introduction of the colonial tent web spider, *Cyrtophora citricola*, to southern Florida, USA as my test system. In Chapter 1, I reviewed the phenomenon of spatial sorting, in which dispersive phenotypes accumulate disproportionately at expanding range fronts. This review was the first to collate empirical examples of different traits that can become spatially sorted, including morphological, physiological, metabolic, behavioral, as well as life history traits. In addition to showing multiple cases across plant and animal taxa that show more dispersive traits at leading edges, reproductive traits such as first age of reproduction and reproductive effort were also subject to change at range fronts, in part due to demographic differences between low density edges and high density core sites.

The consequences of spatial sorting and evolution of traits at leading edges were also considered, in terms of trade-offs between dispersal and other life history traits or quality of life issues. Notably, however, our classic example of a major trade-off between longer limbs in Australian cane toads and incidences of spinal arthritis in leading edge individuals has since been debunked; once thought to be a physiological trade-off to the rapid evolution of longer limbs in this invasive species (Brown et al. 2007), recent work suggests that climate rather than invasion history and leg length better predict this condition (Bower et al. 2018). This highlights how little is currently known about the consequences of spatial sorting and spatial selection on populations. Chapter 1 concludes by discussing the potential ephemerality of leading edge phenotypes once the invasion wave passes former sites. Ultimately, range expansion must end as species encounter barriers that they cannot bypass (e.g. physical barriers like the sea, for a terrestrial species). Little is known from the literature on the effects of spatial sorting over the longer ecological or even evolutionary timescales. With the influx of climate-driven range shifts and invasion-related population expansions, this topic requires greater attention in the future.

In my empirical chapters, I have investigated the American range expansion of the non-native orbweaver, *Cyrtophora citricola*. Despite establishing and spreading in multiple non-native populations in the Americas (Alayon Garcia et al. 2001, Alayon Garcia 2003, Alvares and De Maria 2004, Starr 2005, Viquez 2007), almost nothing is known about these spiders beyond descriptions of their initial discovery, as well as the range expansion of the Cuban population (Sanchez-Ruiz and Teruel 2006). In Florida, they have received likewise little attention beyond an initial survey (Edwards 2006), and my surveys have shown that this species has spread over 250 km along both coasts of Florida. That these two populations likely have originated from the initial core population that these spiders were discovered in lends a unique opportunity to better understand

range expansion processes from the consistency of phenotypic patterns in each population.

Thus, in Chapter 2, I discussed field-collected behavioral data that tested whether personality types show a behavioral cline across the spider's northward expansion gradient in both populations. While I found evidence that many behaviors were indeed assorted across their colonization history, latitude confounded this variable. Importantly, I found that while behaviors related to foraging aggression and activity duration showed consistent behavioral patterns in both the expanding western and eastern populations, exploration and boldness did not. Instead, boldness showed a divergent pattern, with increasingly shy spiders at the western invasion front and increasingly bold spiders at the eastern invasion front. This divergence suggests that despite having originated from a common site, these two populations have been subjected to different selection pressures.

In Chapter 3, I tested the spatial sorting hypothesis and the genetic vs. plastic nature of foraging aggression, exploration/activity, and boldness in *C. citricola* spiders from Florida. I found dispersal tendency to be correlated with exploration and activity. Further, eastern spiders were more dispersive than core and western spiders. Although the spatial sorting hypothesis receives some support in the eastern population, it is evident that other processes have influenced phenotypic assortment and/or selection in the western population. The discovery that individuals with greater dispersal tendencies were indeed, more prevalent at the eastern range edge is important in showing that spatial sorting can occur even in passive dispersers like ballooning spiders. Future work would ideally determine whether selective differences are biotic or abiotic in nature.

The continued expansion of these spiders in Florida, possibly along urban gradients, inevitably raises the question of the fate of these populations when eastern and western populations converge at northern sites. Whereas south central Florida likely represents a matrix of uninhabitable grasslands and swamplands for *C. citricola*, human settlements in inland sites, such as Orlando, Ocala, or Gainesville, represent areas where these two currently separated populations may resume regular gene flow. Since I found the two populations to differ in boldness and exploration, two genetically-based behaviors, it is possible that different genotypes are found at the leading edges of these populations. Any admixture occurring in the near future may have interesting and important consequences for further range expansion, as average dispersers in the western population encounter more strongly dispersive individuals from the eastern population.

In Chapter 4, I used native populations of *C. citricola* as null models with which to understand personality distributions in the invasive range. Counter to my predictions, Florida populations showed no evidence of differing drastically from native Spanish or South African spiders. Strikingly, the core population in Florida actually resembled the native populations more than its invasion front. Overall, I

concluded that this can be due to the relatively static nature of established populations converging on similar personality compositions, since strong environmental and climatic differences occur between southern Florida and Spain and South Africa. In *C. citricola*, I found no evidence that the transportation, introduction, or establishment phases of invasion filtered out certain behavioral phenotypes, potentially due to the plasticity of some of the behaviors assayed. Given the strong differences between the core and leading edge populations in Florida, this suggests that the spreading phase in invasion may create greater phenotypic variation within a population than among native and invasive populations. As range expansion slows and ceases in these populations, I predict that former leading edge sites will phenotypically turnover to resemble the core population, and by association, the native populations, barring stronger locally selective pressures.

Like many study systems with much to offer, the phenomena reported by this dissertation raise a slew of important new research questions. The longevity of leading edge traits, trade-offs between different personality types, and a better understanding of biotic interactions between these non-native spiders and urban heterospecifics will all provide important clues to the future outlook of this spider in Florida.

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VITA

Angela Chuang was born and raised in the sunny hills of Fremont, California. She attended the University of California, Berkeley, where she received a Bachelors of Science in Molecular Environmental Biology and a minor in Forestry and Natural Resources. After a gap year spent happily tracking parrotlets in Venezuela and hunting spiders in the Caribbean and Taiwan, she joined a PhD program at the Department of Ecology and Evolutionary Biology at The University of Tennessee, Knoxville. She graduated with a Doctorate of Philosophy in Summer 2019.